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WINTER HABITAT USE AND ACTIVITY PATTERNS OF NORTHERN FLYING SQUIRRELS IN SUB-BOREAL FORESTS

by

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Abstract

We described winter activity patterns of northern flying squirrels (*Glaucomys sabrinus*) and determined characteristics of nest trees and the surrounding habitats in sub-boreal forests of northwestern British Columbia during the winters of 1996–97 and 1997–98. Nineteen flying squirrels (12 males, 7 females) were fitted with temperature-sensitive radiocollars. We located animals in 82 daytime nests using radiotelemetry techniques and monitored 268 nights of activity using data-logging receivers placed at the base of nest trees. Squirrels used an average of 5.6 ± 0.5 ($\bar{X} \pm SE$; range = 3–10) nest trees per animal. Average nest temperature, as determined by the collar sensors while the animals were in nests, was 39.2 ± 0.1°C (range = 30.9–43.0°C), with no significant differences among animals, tree species, or tree sizes. We observed three aggregations of flying squirrels, which lasted from 3 weeks to 2 months in the 1996 winter. Activity periods in a mild winter (1997) followed a dusk and dawn activity pattern, but activities in a harsh winter (1996) were shifted towards a shorter, single activity bout or two very short bouts in the middle of the night. No long activity bouts (>1.9 h) were observed at very cold temperatures (<-20°C). This adjustment in timing and reduction in the amount of active time during extremely low temperatures likely serve as an energy conservation strategy and may decrease predictability of squirrel activity by predators. Core nest areas used by flying squirrels averaged 2.74 ± 0.62 ha in size; areas were more variable for males (0.86–8.58 ha) than females (0.03–2.23 ha). Characteristics of nest trees were highly variable, suggesting that animals select more for suitable nest sites than for tree size: dbh ranged from 16.7 to 79.0 cm, age

from 42 to 174 years, and tree height from 11.2 to 32.7 m. In comparison to trees that were randomly available in the locale of nest trees, however, animals selected a significant proportion of trees that were larger, older and taller. Forest management activities should give particular attention to retaining nesting structures, such as large snags, large live trees with cavities, and trees with witches' brooms.

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Preface

Current silvicultural practices tend to reduce many of the forest attributes that are believed to be necessary for cavity nesters and other interior forest specialists. New forest harvesting regimes such as patch retention may be able to provide suitable habitat for these species by retaining nesting structures and by maintaining structural diversity within stands. Information about required habitat attributes, however, is needed for effective management. Most wildlife tree studies have concentrated on cavity nesting birds; ecological data collected on mammalian wildlife tree users, such as the northern flying squirrel, will broaden the applicability of wildlife tree prescriptions.

The majority of research on northern flying squirrels has been conducted in west coastal forests of the Pacific Northwest and in the eastern United States. Habitat requirements have not been fully examined in northern boreal ecosystems and few data exist on activity patterns of northern flying squirrels, especially during winter months. Their role as dispersal agents for ectomycorrhizal fungi and arboreal lichens has been proposed, but the extent of the ecological contribution by northern flying squirrels in northern coniferous forests remains undefined.

To investigate the habitat characteristics used by northern flying squirrels in sub-boreal forests during winter, I monitored radiocollared animals in northwestern British Columbia. In Chapter I, I present biological information on activity patterns and movements of northern flying squirrels in relation to ambient conditions. In Chapter II, I present the structural attributes of the nest trees used by this species and the characteristics of the sites surrounding them. Both of these chapters are

intended for publication in peer-reviewed journals. Chapter III incorporates these findings into a forest management context and is intended for dissemination to forest managers as a research extension note.

Chapter I

Winter activity patterns of northern flying squirrels in northwestern British Columbia

INTRODUCTION

The northern flying squirrel (*Glaucomys sabrinus*) is endemic to coniferous forests over a wide range of North America, from Alaska to California, across Canada, and extending to North Carolina (Wells-Gosling and Heaney, 1984). As a cavity nester that is generally mycophagous, its habitat requirements are specific. In winter, northern flying squirrels subsist primarily on arboreal lichens (*Bryoria* spp.) and cached mushrooms or truffles (e.g., *Rhizopogon* spp.; Hall, 1991; Laurance and Reynolds, 1984; Maser et al., 1986; Zabel and Waters, 1997). Flying squirrels use tree cavities and witches' brooms year round for nesting, and typically do not augment the arboreal nests with subnivean resting sites, as do red squirrels (*Tamiasciurus hudsonicus*; Pruitt and Lucier, 1958). Remaining in trees may provide increased protection from predators, such as pine marten (*Martes americana*), which frequently enter subnivean dens occupied by small mammals in winter (Sherburne and Bissonette, 1994). These specific requirements make flying squirrels vulnerable in areas where forested habitats are being degraded, as seen by the decline in populations in the southeastern United States (Urban, 1988).

Northern flying squirrels encounter extremely cold winter temperatures in much of their range, yet they do not hibernate or undergo torpor (Wells-Gosling and Heaney, 1984). Their continual activity throughout winter, coupled with small mass (~150 g) and nocturnal habits, likely necessitate physiological and/or behavioural

strategies that are directly related to thermal conditions and energy conservation. These adaptations are especially needed in winter when the difference between body and ambient temperatures is greatest, and when energy may be critically limiting. Only a few studies conducted on flying squirrels have collected information throughout the year (Gerrow, 1996; McDonald, 1995; Mowrey and Zasada, 1984), but none have specifically examined the activity patterns of the animals during winter.

As part of a study to investigate the habitat characteristics used by northern flying squirrels in sub-boreal forests of British Columbia during winter, we examined activity patterns and movements of the animals. Our specific objectives were 1) to determine the number of nest trees used per animal and how those nest trees differed thermally, 2) to describe winter activity patterns of northern flying squirrels, and 3) to characterize those patterns in relation to ambient conditions (temperature and photoperiod).

METHODS

Study area

The study was conducted at two sites in northwestern British Columbia: the Smithers site, where most data collection occurred, and the Houston site, which was used to complement our sample size during the first field season when rates of trapping flying squirrels were low at the Smithers site. The Smithers site was located in the Smithers Community Forest (54° 43'N, 127° 15'W), 10 km west of Smithers, British Columbia. The Houston site (54° 27'N, 126° 49'W) near Houston,

British Columbia was ~26 km southeast of the Smithers site. Both sites are in the Sub-Boreal Spruce (SBS) biogeoclimatic zone, which is characterized by a cold, continental, humid climate with severe, snowy winters (Pojar et al., 1984; Pojar et al., 1987). Mean annual precipitation exceeds 512 mm; snow fall averages ~200 cm (Environment Canada, 1980).

The Smithers Community Forest, ~4620 ha in size, is a patchwork of stand types resulting from fire disturbance in the 1930's and 1940's. The research site was located on the lower slope of Hudson Bay Mountain, with an average elevation of 850 m. Dominant species included hybrid white spruce (*Picea engelmannii x glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and some trembling aspen (*Populus tremuloides*) and cottonwood (*Populus balsamifera*). The Houston site, with an average elevation of 585 m, had a similar plant species composition, with the addition of paper birch (*Betula papyrifera*), and was surrounded by extensive clear-cuts produced during the last 20 years. Witches' broom rusts (*Chrysomyxa* spp.) occurred on conifers at both sites.

Field methods

Flying squirrels were captured using Tomahawk live traps (Model 201, Tomahawk, WI) in September and October of 1996 and August and September of 1997. Polyethylene stuffing was placed inside the traps to provide thermal protection. Traps were then covered with dark plastic garbage bags and mounted on trees approximately 1.5 m above and horizontal to the ground surface. Traps were baited with a mixture of peanut butter and rolled oats; they were set at dusk

and checked at dawn to minimize the capture of nontarget species (e.g., red squirrels and pine marten). At the Houston site, we established a total of 90 traps in three trapping grids with 50-m spacing. At the Smithers site, we set 156 traps along 7.5 km of an existing trail system, placing a trap on either side of the trail at approximately 50-m intervals.

Captured flying squirrels were transferred from the trap to a cloth and nylon mesh handling cone. We anaesthetized individual animals in a 4-l glass jar by wetting a gauze pad with isoflurane (Aerrane, Ohmeda Pharmaceutical Products, Mississauga, ON) and placing it in the bottom of the jar. An animal was kept in the handling cone for the sedation process so that it could be removed from the jar periodically to ensure adequate oxygen intake. Induction time varied from 5 to 45 min; recovery ranged from 5 to 20 min. Flying squirrels were weighed, sexed, aged (using a combination of mass and colour to determine juvenile or adult age class; Davis, 1963), and ear-tagged (Monel No. 2, National Band and Tag Co., Newport, KY). They were fitted with radiocollars, which weighed 3 g and were composed of a temperature-sensitive radiotransmitter (Model PD-2CT, Hollohill Systems, Ltd., Woodlawn, ON) attached to plastic cable ties and encased in heat-shrink tubing. The transmitter antenna was folded back on itself and placed inside the tubing with the last 2.5 cm of the antenna protruding. We mixed cayenne pepper with an adhesive and applied it to the outside of the collar to minimize chewing by conspecifics. Animals were placed on a hot water bottle during the handling process for warmth and were administered sugar water orally before release to minimize capture stress and prevent hypoglycemia.

Flying squirrels were located in nest trees during the day using a Lotek receiver (Model SRX_400'A', Lotek Engineering Inc., Newmarket, ON) equipped with a visual display of signal strength, which we used to distinguish the nest tree from other trees surrounding it. We also selected two or three animals each day for continuous monitoring and ensured that all animals were monitored routinely (every 1–2 weeks). The data-logging receivers, attached to 12-V sealed, rechargeable, external batteries (Model PS-12150, Power Sonic, Redwood City, CA) in styrofoam-lined storage bins, were placed at the base of nest trees occupied by those animals. Pulse rate of the radio signal (beats/min) received from the collars was directly related to the temperature of the collar. Consequently, when the subject animal left the nest tree, pulse rate of the radio signal declined markedly. Flying squirrels were monitored until mortality or loss of signal (from 2 to 6 months). Only one animal in the first field season was retrapped at the end of the season to remove the radiocollar (see Appendix A). The 1996 field season, referred to as the 1996 winter, occurred from September 1996 to March 1997; the 1997 field season, referred to as the 1997 winter, was from August 1997 to February 1998.

At all nest trees, we recorded whether the tree had a visible nest (cavity, witches' broom, or dray—a constructed nest). We also recorded tree species, height, dbh, and other surrounding habitat measurements (for more details, see Chapter II). If a flying squirrel was present in the nest tree, we noted temperature of the collar. The UTM coordinates of all nest trees were determined using a hand-held base station-correctable GPS unit (March II, Corvallis Microtechnology, Inc., Corvallis, OR). Differential correction of coordinates was made using the PC-GPS

software (Version 2.50a, Corvallis Microtechnology, Inc., Corvallis, OR).

Measurements of air temperature (from a shaded, protected thermistor), wind speed (using a cup anemometer), and solar radiation (obtained with a short-wave Li-cor sensor) were recorded continuously and averaged every 15 min using a CR-21X Micrologger (Campbell Scientific, Edmonton, AB) mounted on a portable weather station in a representative stand at the Smithers site. Dusk was defined as the time at which the Li-cor sensor reading declined to <0.1 W/m^2 at the end of daylight hours. Conversely, dawn was defined as the time at which the sensor reading increased to >0.1 W/m^2 following a period of complete darkness. Phases of the moon and the time of moon rise were obtained from U. S. Navy astronomical data, using Ketchikan, Alaska as a close approximation for Smithers, British Columbia (http://aa.usno.navy.mil/AA/data).

During the 1996 field season, we attempted to determine the direction of nightly foraging bouts from the nest tree by flying squirrels. We used headlamps to observe animals and placed data-logging receivers at random locations 50–150 m away from the nest trees of the selected animals. In the 1997 field season, we conducted nighttime telemetry on three animals (four attempts per animal) using triangulation to determine the size of the area used during foraging activities. Simultaneous bearings were taken from known locations by two observers at 5-min intervals, starting just before an animal became active after dusk. Monitoring continued until the animal moved out of range or returned to a nest tree for an extended period of time.

Statistical analyses

An alpha level of 0.05 was assumed for all analyses. Unless otherwise stated, all means are presented as $\bar{X} \pm SE$. We used analysis of variance (ANOVA; Sokal and Rohlf, 1995) to determine if there were differences in the number of nest trees used by flying squirrels between sites, years (to accommodate changes in habitat productivity), and sexes; sex was nested within either site or year. We limited our analysis to habitual nest trees, defined as trees in which an animal was located more than once. To determine if the number of nests used by flying squirrels declined over time in response to the increasing energetic demands of winter, we used a repeated measures ANOVA (Sokal and Rohlf, 1995) to test for differences in the number of nests used per month among months and between years, sexes, and seasons (fall [October through December] and winter [January and February]). Only animals for which we had data spanning all months were included ($n = 7$) and differences between sexes were examined within the same year (1997; $n = 5$). Animals located <10 times ($n = 4$) were excluded from analyses of the number of nest trees. We used correlation analysis (Moore and McCabe, 1993) to examine relationships between the number of nest trees used per animal and 1) the number of times an animal was located, and 2) the duration of time over which observations for that animal occurred. Distances between nest trees used consecutively and between nighttime telemetry locations were calculated using the PC-GPS software (Version 2.50a, Corvallis Microtechnology, Inc., Corvallis, OR). We used ANOVA to test for differences in nest temperature by animal ($n = 19$) among the individual nest trees and for differences in nest temperature between

cavities and outside nests (witches' brooms and drays). Correlations were used to examine relationships among nest temperature (i.e., temperature of the radiocollar on a flying squirrel in the nest) and each of the following: ambient temperature, tree height and dbh. We used a non-stepwise multiple regression (Sokal and Rohlf, 1995) to examine the influence of ambient temperature and nest tree characteristics on nest temperature, using all data, by sex, and within each species of nest tree. Because of the strong correlation between tree height and dbh ($r = 0.71$, $P < 0.001$), only dbh was used in the model. For each animal, a separate ANOVA was run for each nest tree used for aggregations of flying squirrels to determine if there were differences between nest temperatures prior to and during aggregation (nest sharing) with other radiocollared animals. Pearson Chi-square (χ^2) contingency analysis (Everitt, 1977) was used to test if the distributions of time spent away from nest trees differed between years. We tested whether the timing of activity by flying squirrels was correlated with moon phase or the time of moon rise. Correlation analysis was also used to examine the relationship between the length of activity bouts and ambient temperature in each winter. Triangulated nighttime telemetry locations and error polygons were calculated using TRIANG (White and Garrott, 1990). Descriptive statistics, ANOVAs, correlations, multiple regressions, Pearson Chi-square analysis, and graphical representations were completed using STATISTICA (StatSoft, Inc., 1997).

RESULTS

Nineteen adult northern flying squirrels were radiocollared over the two field seasons: eight males and four females in 1996 (725 trap nights), and four males and three females in 1997 (832 trap nights). The average body mass of the animals at the time of collaring was 145.3 ± 2.4 g (see Appendix A). Generally, we located individuals 1–3 times per week, although three animals located in a remote area of the Houston site were located only 3–4 times monthly after snowfall. In the 1996 field season, animals were located in nest trees in the daytime 303 times with 7–82 locations per animal; in the 1997 field season, animals were located 265 times (29–50 locations per animal).

Nest use

Squirrels used an average of 5.6 ± 0.5 nest trees per animal (range = 3–10). When occasional nest trees, defined as trees in which an animal was located only once, were removed from the data set, the average number of nest trees used habitually per animal was 3.8 ± 0.4. There were no differences in the number of habitual nest trees per animal between sites, years, or sexes (all $P > 0.182$). As determined by repeated measures ANOVA, the number of nest trees used per month did not differ among months, or between years or sexes (Fig. 1). There was a trend for the number of trees used per month in fall to be higher than in winter, though again not significantly ($F = 4.89$, $d.f. = 1,6$, $P = 0.069$), for the seven animals that were alive throughout the 5-month period.

On 280 occasions, individual flying squirrels were relocated on consecutive days. For 92% of those observations, animals stayed in the same nest tree the

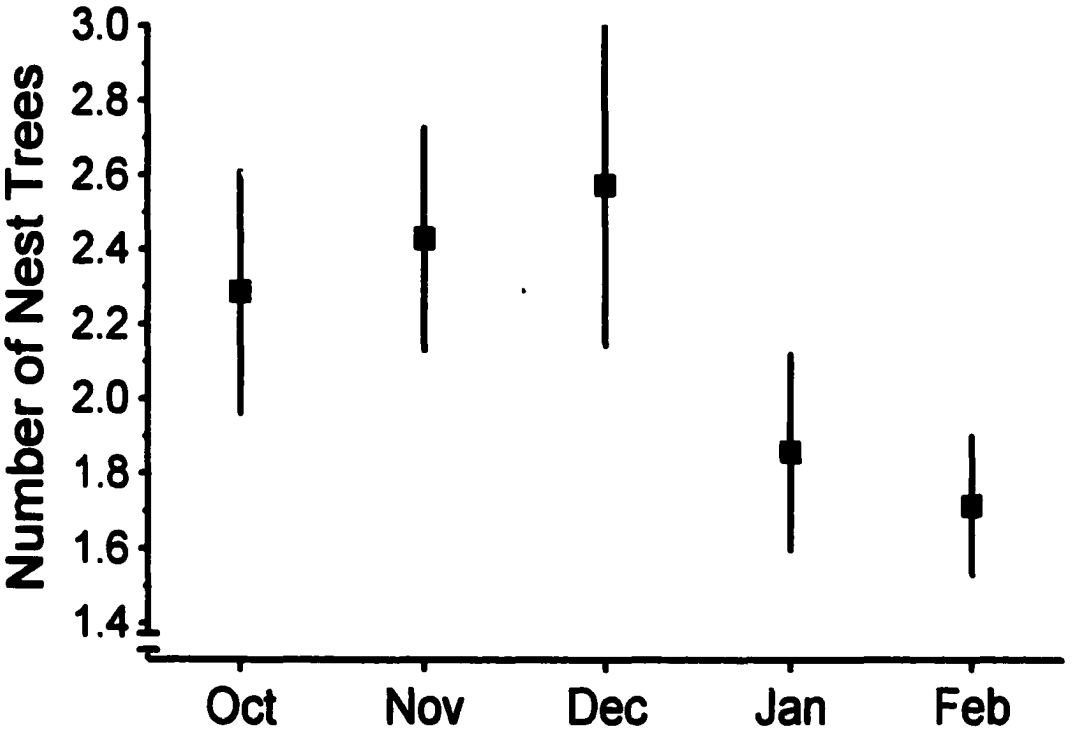

Fig. 1. Average number of nest trees (± *SE*) used monthly during fall (Oct–Dec) and winter (Jan–Feb) by seven northern flying squirrels in northwestern British Columbia.

second day. For the remaining observations, where animals moved to a new nest tree, the average distance moved was 163.2 ± 21.9 m, but ranged from 7.5 to 362.7 m. There was no correlation between the number of nest trees located per animal and the number of observations per animal (r = 0.55, P = 0.058) or the time span over which observations occurred (r = 0.26, P = 0.394).

The 1996 winter was considerably more harsh than that of 1997, in terms of temperature extremes and snowfall. The 1996 winter was characterized by many periods of extremely cold weather, with a minimum temperature of -35.8°C (25 January). The first lasting snowfall (>10 cm) occurred on 9 November. The 1997 winter was milder, with -16.8°C (18 December) as the lowest recorded temperature and the first lasting snowfall not occurring until 24 November. Snow depth at the weather station in the 1996 winter (1.12 m in mid-January) was approximately twice that of the 1997 winter (0.56 m in mid-January).

Only 14 nests in trees were visible from the ground: 11 witches' brooms, 2 drays, and 1 cavity. All other nests (n = 68) were presumed to be in cavities. Average nest temperature, as determined from the temperature-sensitive radiocollars, was 39.2 ± 0.1°C (n = 529), ranging from 30.9 to 43.0°C. Only one randomly selected nest temperature for an individual was used per 24-h period in these calculations. There were no differences among individual nest trees, examined for each animal (all P > 0.308). Cavities had a higher average nest temperature (39.2 ± 0.1°C, n = 412) than outside nests (38.7 ± 0.2°C, n = 108; F = 7.346, d.f. = 1,518, P = 0.007), although means differed by only 0.5°C. Nest temperature was not correlated with ambient temperature, tree height, which ranged

from 11.2 to 32.7 m, or tree dbh (16.7–79.0 cm; all $P > 0.05$). Air temperature and tree dbh were not good predictors of nest temperature using all data, even though the multiple regression was significant ($R^2 = 0.052$, $P < 0.001$); similar results were obtained when analyzed within males ($R^2 = 0.084$, $P < 0.001$) and within females ($R^2 = 0.086$, $P < 0.015$). Within nest trees of the same species, only hybrid white spruce and lodgepole pine showed a significant relationship among nest temperature, air temperature, and tree dbh, though again with little predictive value (spruce: $R^2 = 0.124$, $P < 0.001$; pine: $R^2 = 0.073$, $P < 0.004$). Further, there was no difference between the average nest temperature of individual animals prior to and during times of aggregation with other radiocollared animals (all $P > 0.178$).

Aggregation

Three separate periods of aggregation by radiocollared animals were observed in the first field season. One aggregation involved two females and one male at the Houston site, beginning in the first week of November 1996. The three animals aggregated in a witches' broom on a hybrid white spruce (dbh = 18.6 cm, height = 17.5 m) for several nights. Following the return of one of the females to its previously used nest trees, the remaining female and male nested together in three subsequent hybrid white spruce trees (dbh = 25.8, 19.9, 22.5 cm; height = 21.8, 17.7, 20.0 m, respectively), one of which had a witches' broom. The lowest nightly temperature at the onset of the aggregation was -6.5°C; the lowest recorded temperature during the aggregation period was -25.1°C. Another aggregation period involved a male and female at the Smithers site, beginning mid-October and

lasting until late November. The animals occupied three nest trees together (two lodgepole pine, dbh = 21.6 and 31.1 cm, height = 19.9 and 25.5 m, respectively; one hybrid white spruce, dbh = 24.7, height = 19.3 m), two of which were used by the female prior to the aggregation period. The lowest nightly temperature at the beginning of this aggregation was -1.6°C; lowest nightly temperatures during the period ranged from -26.9 to 0.4°C. The final aggregation consisted of two males at the Houston site and lasted over 2 months with three nest locations, beginning in early October. Two of the shared nests were large hybrid white spruce trees (dbh = 43.5 and 44.6 cm, height = 28.8 and 29.8 m, respectively); the third nest site was a clump of branches and needles, possibly built into a dray, where two dead and one live tree leaned together. For each of the aggregation periods we observed, aggregation among radiocollared animals ended upon the death of the other partner(s) or when the radio-signal ceased. In addition to aggregations, two nest trees were used by two animals, though not together.

Activity patterns

We recorded 268 days and nights of activity patterns using the data-logging receivers placed at the base of nest trees. Radiocollared flying squirrels never left their nests during daylight hours. During nighttime activity periods, the amount of time that animals were away from nest trees, as recorded by each observation of leaving and reentering the nest, ranged from 0.52 to 13.7 h. The distributions of the time periods away from nest trees significantly differed between years (Fig. 2; *Pearson* $\chi^2 = 76.797$, *d.f.* = 6, $P < 0.001$). Given those distribution patterns, in which >70% of our observations showed that flying squirrels returned to the nest

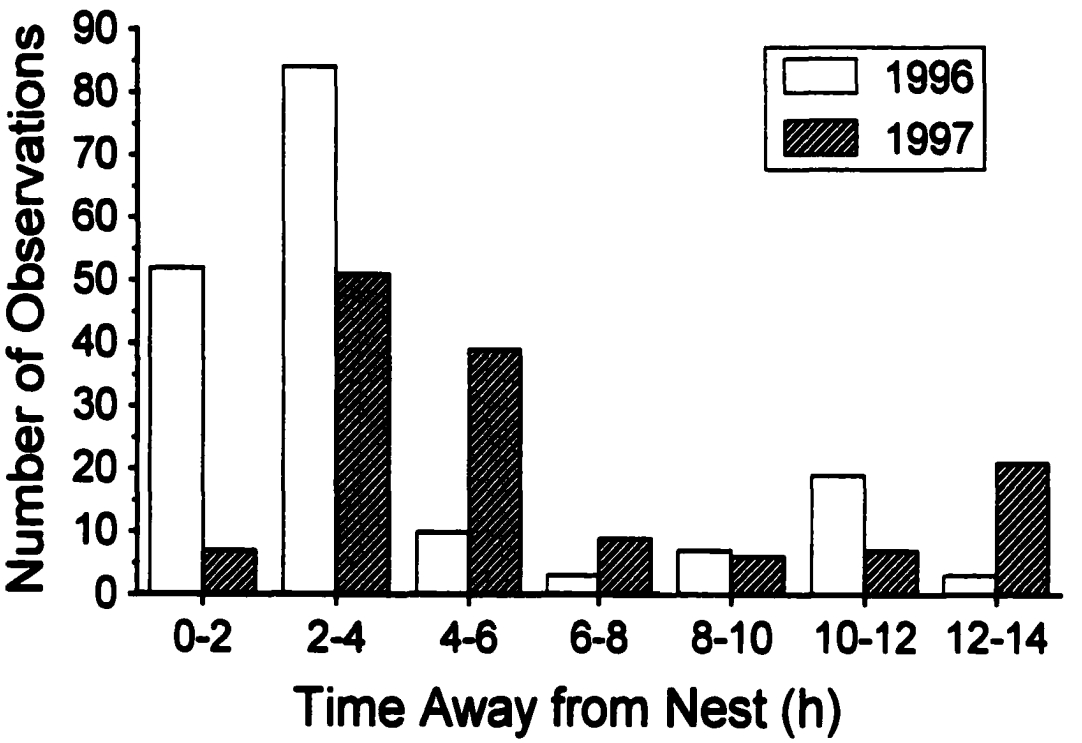

Fig. 2. Amount of time spent away from nest trees by northern flying squirrels during nightly activity periods in a harsh winter (1996) and a mild winter (1997).

tree within 6 h, and coupled with the likelihood that greater times away from the nest included time spent at other nest trees (Weigl and Osgood, 1974), we set 6 h as a conservative maximum amount of time for a single activity period.

In 179 of the recorded nights of activity patterns, animals returned to the original nest tree within 6 h of first leaving; in the remaining observations, animals either did not return to the nest tree or did not return until just before dawn (>6 h since leaving). Of those 179 cases, 42.4% showed two activity periods per night: one beginning within 2 h after dusk and another period of activity commencing later in the night and ending within 2 h before dawn. Another 49.7% of the observations showed an activity period or periods during the middle of the night. The remaining nighttime observations were composed of a combination of dusk, mid-night, and/or dawn activity periods. When analyzed by year, 72.4% of the observations from the 1996 field season contained only one period away from the nest, while 76.3% of the observations in the 1997 field season consisted of two periods away from the nest. The two field seasons also differed in the timing of nightly activity: the time of leaving and the time of return to nest trees were much more variable and often later in the night in the 1996 winter than in the 1997 winter, which followed a predominantly dusk/dawn activity pattern (Fig. 3). Deviations from a dusk/dawn activity pattern in both winters were observed only after the temperature dropped sharply and was <-10°C. This occurred in early November during the 1996 winter and not until early December in the 1997 winter (Fig. 4). The timing of activity was not correlated with moon phase or the time of moon rise (both $P > 0.05$).

The length of activity bouts away from the nest was positively correlated with

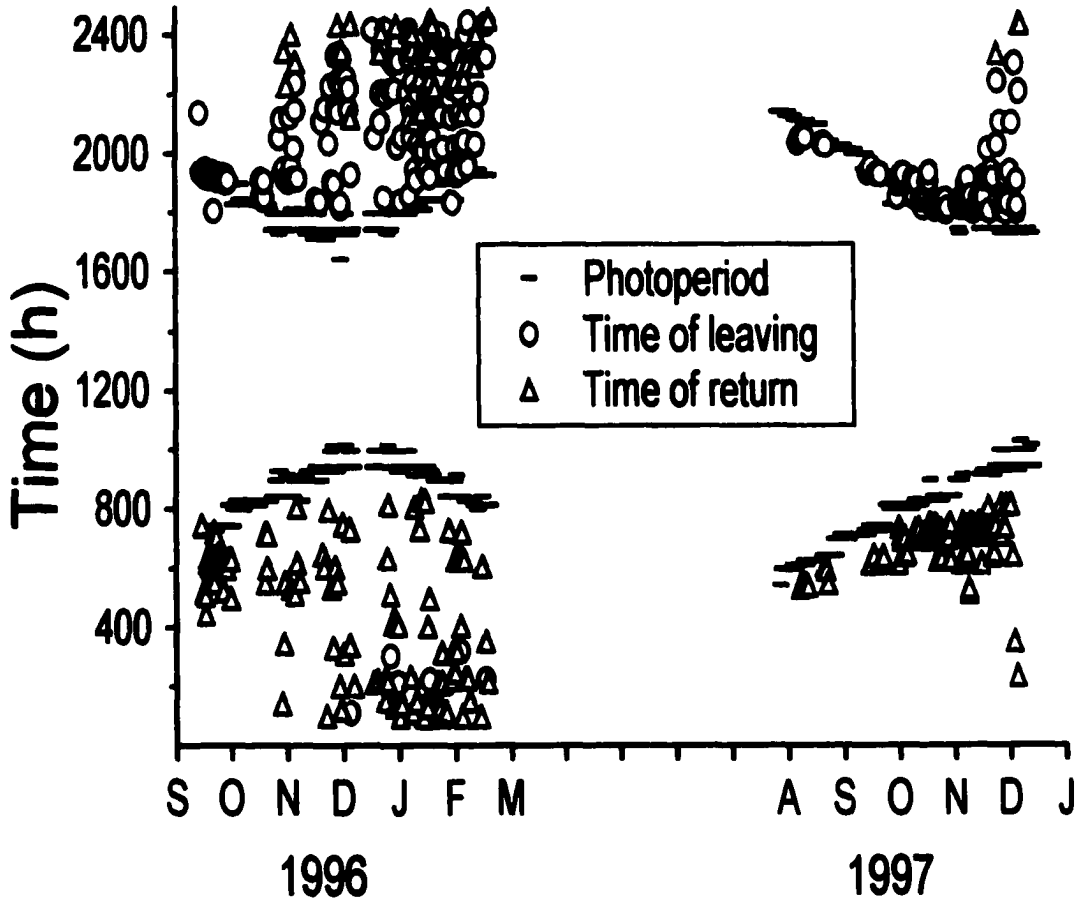

Fig. 3. Times of first departure and last return by flying squirrels to a nest tree in relation to photoperiod (time of the onset of darkness or onset of light) during 2 winters in northwestern British Columbia. X-axis labels indicate the middle of each month.

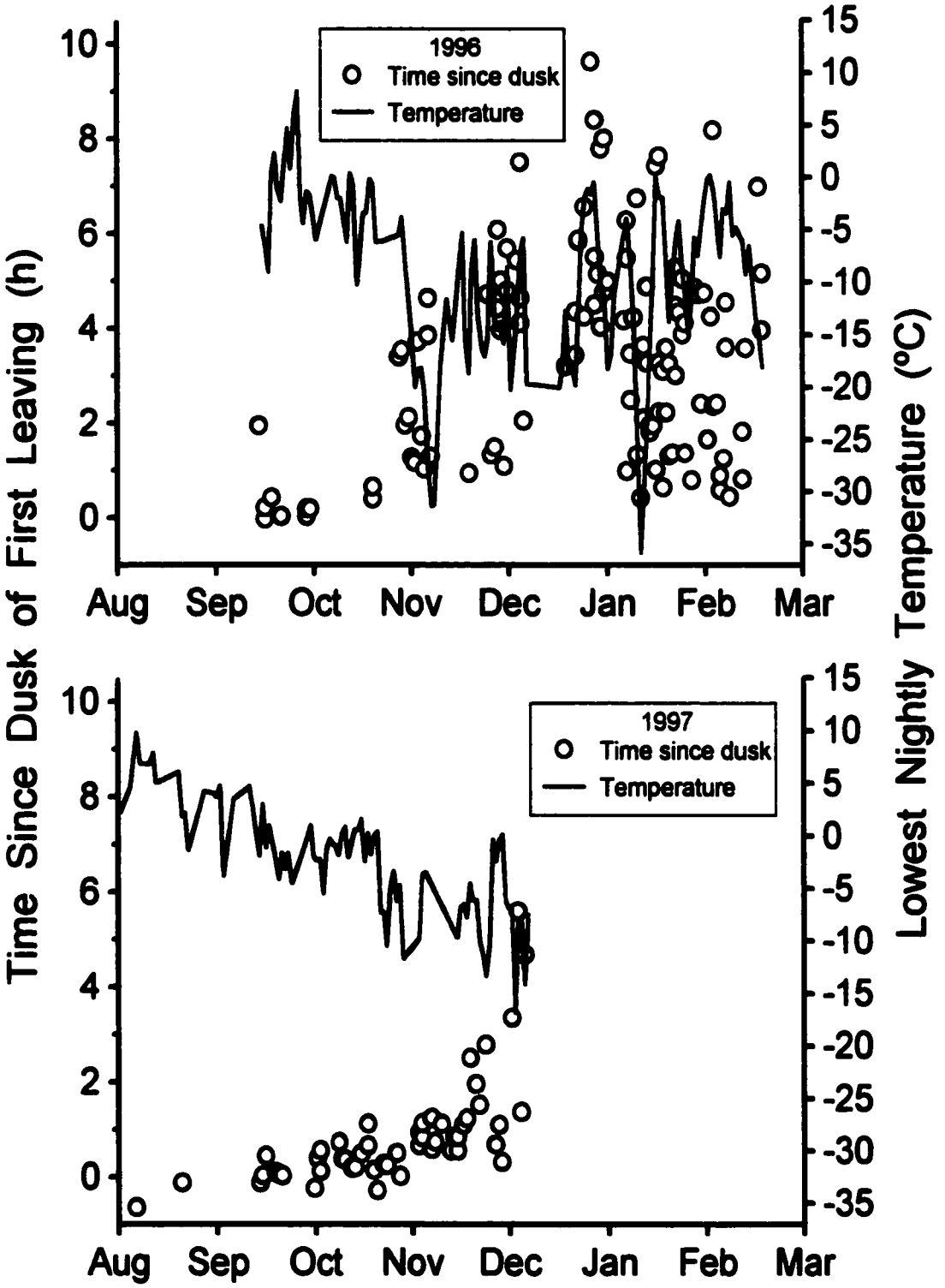

Fig. 4. Timing of the onset of nightly activity by northern flying squirrels in relation to minimum nightly temperatures during the harsh 1996 winter and the mild 1997 winter in northwestern British Columbia. X-axis labels indicate the middle of each month.

air temperature in the 1996 winter (r = 0.46, P < 0.001, n = 147), but not in the 1997 winter (r=0.11, P = 0.319, n = 88; Fig. 5). At very cold temperatures (<-20°C) in 1996, there were no long activity bouts (maximum bout length = 1.9 h), whereas at warmer temperatures, the time spent away from a nest tree was generally more variable. A similar trend was observed after summing all active bouts per night (Fig. 6). At temperatures <-20°C, the total time absent from the nest ranged from 1.4 to 1.9 h, regardless of whether the animal had one nightly activity bout (n = 3) or two bouts (n = 3). Three activity bouts during a single night were only observed in the 1997 winter, and occurred at temperatures above -10°C (n = 5). The total time spent away from the nest tree per night at temperatures >-10°C was highly variable, and ranged from 1.3 to 11.0 h (Fig. 6; males: 1.3–10.2 h, females: 4.0–11.0 h).

Attempts to follow animals at night were unsuccessful because observer movements and noise likely influenced animal movements. Nighttime data-logging efforts at random locations around nest trees in the 1996 season also were not successful in defining foraging areas. We were able to determine only the general direction the animal travelled in, but not the distance or location of a specific area where the animal spent most of its active time. In the 1997 winter, triangulation bearings were extremely variable and had too much error to reliably estimate the movements of the animals outside their nest trees. Although movements were calculated to be >400 m from nest sites before animals moved beyond the range when signal strength was too low to determine accurate bearings, the size of error polygons ranged from 5.1 m^2 to 1.75 ha ($\bar{X} \pm SD$ = 0.07 ± 0.21 ha).

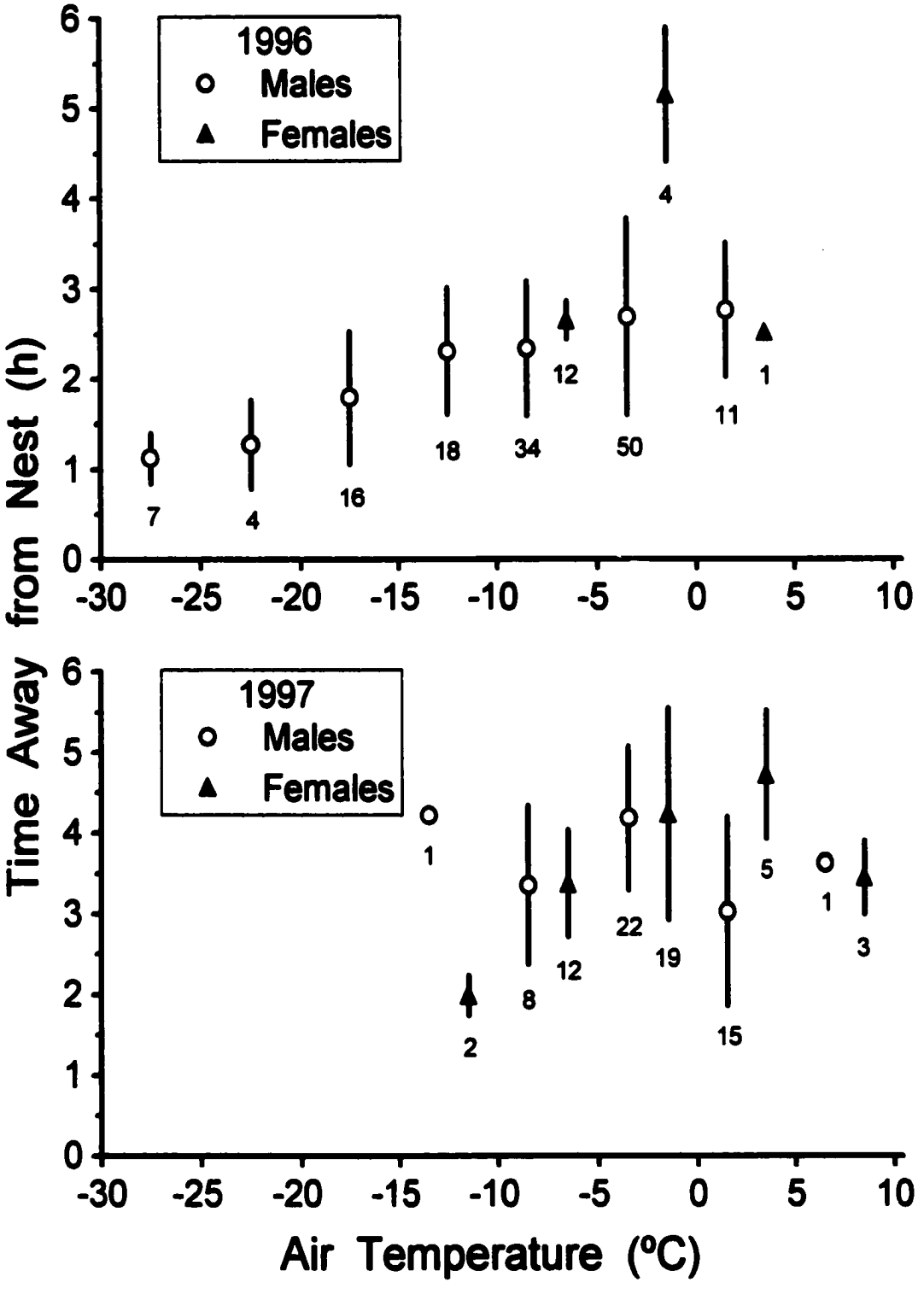

Fig. 5. Length of activity bouts (± *SD*) in relation to air temperature for male and female flying squirrels during 2 winters in northwestern British Columbia. Plotted X-values are lengths of bouts averaged within each 5°C increment; numbers indicate the sample size.

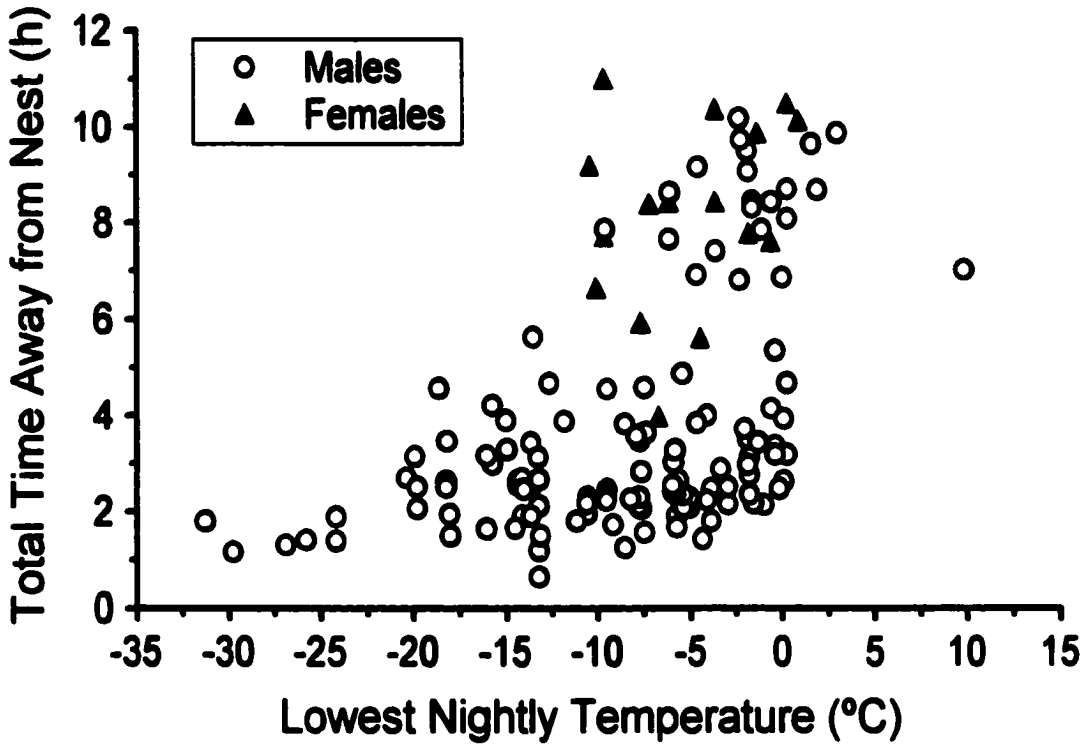

Fig. 6. Total time spent away from nest trees per night (combining all bouts <6 h in length within the same night) by male (n = 12) and female (n = 7) northern flying squirrels in relation to the lowest ambient temperature of the night.

DISCUSSION

Trapping efforts were completely unsuccessful in warm summer months (e.g., July). Animals began entering traps only after nightly temperatures began to drop to near 0°C, as noted by other researchers in the area (J. D. Steventon, pers. comm.). Food resources, especially mushrooms and truffles on the ground, were likely abundant enough during summer that animals were not easily trapped.

Nest use

The use of multiple nests by northern flying squirrels has been suggested to be an adaptive response to variable and patchily-dispersed food abundance (Carey et al., 1997). The average number of nests used by animals in our study was similar to that reported in coastal forests of western Oregon ($\bar{X} \pm SE = 6.1 \pm 0.6$; Carey et al., 1997), but less than noted in interior forests of Alaska ($\bar{X} > 8$; Mowrey and Zasada, 1984). Although our sample size may have been too low or the variability too high to detect the change statistically, the number of nests used per month during winter months tended to decline, which is consistent with Carey et al. (1997). The use of nests may decline between summer/fall months, when animals forage on widely dispersed mushrooms, and winter months, when animals rely on more readily available food sources, such as arboreal lichens or cached fungi. It is not known whether flying squirrels cache fungi themselves, but Mowrey and Zasada (1984) frequently observed flying squirrels stealing cached fungi from red squirrel middens. Molds were found in diet samples from gastrointestinal tracts of northern flying squirrels in winter and fecal pellets in spring and summer from the boreal

mixedwood forests of Alberta, suggesting that the food had been cached prior to consumption (R. S. Currah, pers. comm.). The number of nests used by flying squirrels may also decline as an adaptive response to cope with changes in climatic conditions and increasing energy demands. The average distance moved between consecutive daily locations was larger in our study than in central Oregon ($\bar{X} \pm SE$ = 71 ± 1.6 m; Martin and Anthony, 1999), but similar to the distance between consecutive nest trees, though not always located on consecutive days, reported for coastal forests of Oregon (Carey et al., 1997).

Northern flying squirrels were capable of sustaining high nest temperatures over a wide range of different nest trees. We expected that trees of larger diameter with thicker bark and wood could minimize temperature fluctuations, that tall trees in exposed conditions would show greater fluctuations, and that different tree species could show differences in thermal properties. We were unable to detect any of these differences, and suggest that the sustained high temperature recorded in nests was most likely caused by the sleeping position of the animals. We observed that when a flying squirrel was sedated or arousing from sedation, it tended to curl into a ball with its tail wrapped over its head. Therefore, with the temperature sensor of the radiocollar positioned under the chin of the animals, the temperature readings from inside nests were very close to body temperature, which was recorded at 39°C for the closely related southern flying squirrel (*Glaucomys volans*; Neumann, 1967). Similarly, Weigl and Osgood (1974) reported that nest temperatures, as determined by temperature-sensitive radiocollars, varied only 1–3°C regardless of air temperature. In our study, temperatures in cavities and

brooms were statistically different, but both means were within 0.5°C of 39°C. We did not obtain characteristics of the nest cavities (or brooms or drays) to avoid abandonment of a nest tree by flying squirrels (Carey et al., 1997). Although we were unable to determine the thermal value of different nest trees used by flying squirrels, it is apparent that animals were able to maintain high body temperatures in each nest they chose. Animals likely augment the thermal value of nests with nest lining, such as mosses and lichens, or by aggregating (Stapp et al., 1991).

Aggregation

Our observations of aggregating flying squirrels were limited to radiocollared animals. There may have been non-collared animals that nested with our subject animals, although we were not able to document these occurrences. From our study and others, aggregations of flying squirrels do not appear to be regulated solely by thermal constraints. In our study, each aggregation began after the minimum nightly temperature was below freezing but before temperatures were extremely low, which is similar to the observations from interior Alaska (Mowrey and Zasada, 1984) and western Oregon (Carey et al., 1997). Aggregations of northern flying squirrels have been observed year-round in New Brunswick (Gerrow, 1996). For southern flying squirrels, aggregations peaked in January, but were not restricted to cold months even in warm climates (Layne and Raymond, 1994). Using captive animals, Stapp et al. (1991) found that aggregations of southern flying squirrels were correlated with temperature and that aggregation reduced energy expenditures by 26–33%. Therefore, while aggregating may be adaptive for cold weather, it is not necessarily confined to winter months and may also serve a

social role (Gerrow, 1996).

Maser et al. (1981) reported that aggregating animals were separated by sex, but more recent studies have observed different combinations of sexes aggregating together (Carey et al., 1997; Gerrow, 1996). Our study also showed different combinations of radiocollared individuals within aggregations. Aggregating animals frequently switched to different nest trees together, though they were not always active and absent from a given nest at the same time. In the case of use of the same nest tree by different animals that were not aggregating, one tree was used by a male in the first field season and by a female in the second field season. The other tree was used by a male in the second field season, then abandoned and taken up by another male; data-logger readings showed one occasion where the first male returned to the tree shortly after the second male left, though the first male remained in the nest only 45 min. These behavioural observations show that nest trees can be shared concurrently, used by more than one animal within a season, and used across years by different animals.

Activity patterns

Northern flying squirrels adjusted the duration and timing of nocturnal activity periods in response to the onset of darkness or light and air temperature. Few studies have quantified the duration of activity bouts for flying squirrels, and no values have been reported for animals in the northern regions of their geographic distribution. In Pennsylvania and North Carolina during summer, Weigl and Osgood (1974) noted that flying squirrels were absent from nests for an average of 118 min (range = 53–225 min) in the activity bout following dusk and 76 min (range =

38–110 min) in the activity period before dawn. In our study, the duration of activity bouts also was variable at warm temperatures, but condensed during periods of extreme cold. This trend was observed in the 1996 field season, when there were no long activity bouts and the total time spent away from nests per night was less at extremely cold temperatures; and between field seasons, when a shift towards shorter bout lengths was observed in the harsh 1996 winter (Fig. 2). The high temperature differential between body temperature and low ambient temperatures likely reduces the time that animals are able to spend outside the nest per activity bout. Nonetheless, flying squirrels were active each night to some extent throughout both winters regardless of ambient temperatures.

The timing of activity by flying squirrels in relation to photoperiod has been studied more extensively. Timing of activity may be slightly variable among animals, but generally is consistent within animals (Weigl and Osgood, 1974). In Oregon, animals became active 70.4 ± 10.8 min ($\bar{X} \pm SD$, $n = 20$) after sunset in late summer (Witt, 1992). In West Virginia, Urban (1988) reported two peaks in nightly activity: one at 1–3 h after sunset and another at 7–10 h after sunset. Captive animals also were observed to become active 35.4 ± 2.1 min ($\bar{X} \pm SE$; range = -53–117) after sunset and cease activity within an hour before sunrise, with activity occurring earlier in summer and later in winter in relation to sunset (Radvanyi, 1959). Our observations from the mild winter field season of 1997 (typically with two active bouts per night) are similar to those reported from studies further south. Deviations from the general biphasic pattern of nighttime activity (Wells-Gosling and Heaney, 1984) have not been reported previously, although the

timing of activity was delayed by high winds or rain in Pennsylvania (Weigl and Osgood, 1974) and the percentage of time flying squirrels were active decreased slightly when temperatures were <0°C or precipitation was occurring in West Virginia (Urban, 1988).

The activities of northern flying squirrels observed in the harsh 1996 winter showed adjustments to the more common biphasic dusk/dawn pattern. Animals shifted towards a shorter, single activity bout or two very short bouts in the middle of the night instead of two bouts at dusk and dawn, respectively. Pre-dawn temperatures were typically the lowest each night; therefore, a shift in the timing of activity would potentially lessen energetic demands. We suggest that this adjustment and limiting of the amount of active time during extreme temperatures likely serve as an energy conservation strategy. Further, if animals are indeed using lichens for nest materials, as Hayward and Rosentreter (1994) observed in the Rocky Mountains of Montana and Idaho, they could consume lichens in the nest as a highly digestible cached food instead of foraging outside the nest. Stapp (1992) suggested that the relatively low metabolic rate and conductance seen in southern flying squirrels were adaptive for the greater energetic costs incurred by being active during winter, but similar studies have not been conducted on northern flying squirrels. Stapp (1992) also emphasized behavioural adaptations such as reduced foraging activity at low temperatures, aggregating, and food caching as additional means to reduce energetic costs. An additional benefit from altering the timing of activity bouts in harsh winters may be predator avoidance. Pine marten have been reported to be totally inactive during periods of extreme cold (<-25°C),

followed by surges of activity when temperatures rise (Buskirk, 1983; Fredericksen, 1990). Zielinski et al. (1983) suggested that marten synchronize the timing of their activity with that of their prey. Variability in the timing of leaving by flying squirrels from the nest may decrease predictability of squirrel activity by predators.

Many nocturnal species, including desert kangaroo rats (*Dipodomys merriami*; Daly et al., 1992) and white-tailed jackrabbits (*Lepus townsendii*; Rogowitz, 1997), exhibit decreased activity levels in relation to moonlight. In kangaroo rats, this behavioural shift occurs to avoid nocturnal predators that gain an advantage with increased nighttime illumination (Daly et al., 1992). Radvanyi (1959) found that activity of captive northern flying squirrels followed the lunar cycle: animals decreased the intensity of nightly activity during the brightest part of the lunar cycle, although the timing of activity was not affected. In our study, we did not observe a relationship between activity and lunar phase. Our observations, however, were only able to detect the timing of activity and not the intensity. Thick forest canopies may reduce the amount of moonlight illumination reaching the ground by as much as 99% (Radvanyi, 1959). If the illumination was negligible due to canopy effects (>70% canopy closure in our study; see Chapter II), animals in our study may not have exhibited the same reduction in activity that was observed in captive animals.

Nighttime telemetry on flying squirrels has been partially successful in some studies (Gerrow, 1996), though noise and presence of an observer may influence animal movements (Witt, 1992). In our study, after preliminary attempts to follow flying squirrels during activity bouts, we believed that the activities of the animals

were being modified and determined by our presence, and, therefore, we ceased observations. Triangulation has also been used reliably to determine nighttime locations of northern flying squirrels (Martin and Anthony, 1999) and our triangulation efforts would have been improved with a third observer.

In summary, northern flying squirrels exhibit considerable flexibility in their ability to occupy a wide range of environmental conditions. In the boreal forest ecosystem, flying squirrels used behavioural strategies to contribute to winter survival. They sustained high temperatures in nest cavities and nest structures used for resting, regardless of tree size or species. Nocturnal activity periods away from nests varied with photoperiod and air temperature, presumably in response to energetic constraints and pressures of predation. Physiological adaptations that allow animals to limit energetic costs, which may be similar to those of the southern flying squirrel, should be examined. We recommend that subsequent studies address the role of lichens in providing thermal protection in nests and the extent to which they serve as a cached food resource to help balance energy demands. Studies should also examine the extent to which flying squirrels consume cached mushrooms in winter and the links between consumption and movement of fungi by flying squirrels in boreal forests.

Chapter II

Winter habitat and characteristics of nest trees used by northern flying squirrels in a sub-boreal forest of northwestern British Columbia

INTRODUCTION

The northern flying squirrel (*Glaucomys sabrinus*) occupies forested ecosystems across North America, from Alaska and much of Canada to as far south as northern California in the west and North Carolina in the east (Wells-Gosling and Heaney, 1984). Relatively few ecological studies have been conducted on this species because of its nocturnal habits and small mass (~150 g). As a cavity nester that is generally mycophagous, the northern flying squirrel generally has been considered to be a habitat specialist, dependent on old coniferous forests for both shelter and food. The species forages extensively on highly digestible mushrooms and supplements its diet with arboreal lichens when mushrooms are unavailable (Hall, 1991; Laurance and Reynolds, 1984; Maser et al., 1986; Zabel and Waters, 1997). Consequently, northern flying squirrels potentially serve a key role in the maintenance of forest health by dispersing the spores of mycorrhizal mushrooms (e.g., *Rhizopogon* spp.) and fragments of arboreal lichens (e.g., *Bryoria* spp.; Fogel and Trappe, 1978; Hayward and Rosentreter, 1994; Carey et al., 1999). Most recent attention has focused on its role as the main prey species of the endangered spotted owl (*Strix occidentalis caurina*) in the U. S. Pacific Northwest (Carey et al., 1997; Martin, 1994).

Small changes in forest structure may have significant impacts on habitat specialists. The extent of old-growth habitat specialization by northern flying

squirrels in coastal forests has been called into question recently by studies showing that the species is capable of subsisting in second-growth forests (Carey, 1995; Martin, 1994; Rosenberg and Anthony, 1992). Nonetheless, populations of northern flying squirrels have declined in the southeastern United States due to loss of forested habitat (Urban, 1988). A similar trend has been observed for the ecologically similar eastern flying squirrel (*Pteromys volans*) in Finland (Hokkanen et al., 1982; Mönkkönen et al., 1997). In boreal ecosystems, very little is known about the specific habitat requirements of northern flying squirrels. Only two northern studies have been reported: one in the boreal forests near Fairbanks, Alaska (Mowrey and Zasada, 1984) and the other in mixedwood stands in Alberta (McDonald, 1995). There is a need for detailed research focusing on habitat requirements in areas not characterized by old-growth forests and during winter months, which are the most energetically stressful time of year for small species in northern temperate regions.

To better understand habitat requirements during critical winter months, we investigated the size of the core nest areas and the characteristics of the nest sites used by northern flying squirrels during winter in northwestern British Columbia. Specific objectives of the study were to 1) identify the structural attributes of nest trees, 2) determine how these features compared with randomly selected locations, 3) quantify the frequency of use of nest trees within the core nest areas used by animals in winter, and 4) examine the distribution of nest trees among the ecosystem types and seral stages of the study area.

METHODS

Study area

The study was conducted at two sites in northwestern British Columbia: the Smithers site, where most data collection occurred, and the Houston site, which was used to complement our sample size during the first field season when rates of trapping flying squirrels were low at the Smithers site. The Smithers site was located in the Smithers Community Forest (54° 43'N, 127° 15'W), 10 km west of Smithers, British Columbia. The Houston site (54° 27'N, 126° 49'W) near Houston, British Columbia was ~26 km southeast of the Smithers site. Both sites are in the Sub-Boreal Spruce (SBS) biogeoclimatic zone (Pojar et al., 1987).

The Smithers Community Forest, ~4620 ha in size, experienced fire disturbance in the 1930's and 1940's. It is characterized by pockets of old-growth stands and veteran trees scattered throughout younger stands. The study area was located on the lower slopes of Hudson Bay Mountain, with an average elevation of 850 m. Dominant species were hybrid white spruce (*Picea engelmannii x glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and some trembling aspen (*Populus tremuloides*) and cottonwood (*Populus balsamifera*). The Houston site, at an average elevation of 585 m, had a similar plant species composition, with the addition of paper birch (*Betula papyrifera*), and a similar disturbance history. The site was surrounded by extensive clear-cuts produced in the last twenty years. Witches' broom rusts (*Chrysomyxa* spp.) were found on conifers at both sites.

Field methods

Nineteen northern flying squirrels were trapped in Tomahawk live-traps (Model 201, Tomahawk, WI) and fitted with temperature-sensitive radiocollars (Model PD-2CT, Hollohill Systems, Ltd., Woodlawn, ON) in September and October of 1996 and August and September of 1997 using the protocol outlined in Chapter I. We located the flying squirrels in nest trees during the day using a Lotek receiver (Model SRX_400'A', Lotek Engineering Inc., Newmarket, ON) equipped with a visual display of signal strength, which we used to distinguish the nest tree from other trees surrounding it. Animals were monitored 1–3 times weekly until mortality or loss of signal (2–6 months). Three animals located in a remote area of the Houston site were located only 3–4 times monthly after snowfall.

For each nest tree, we collected the following measurements in the fall or winter when the tree was being used by one or more radiocollared animals: 1) when and how often the site was used, 2) tree species and, when possible, nest type (cavity, witches' broom, or a constructed nest [dray]), 3) tree height, measured with a clinometer, and nest height, if visible, 4) tree diameter at breast height (dbh), 5) tree age, using an increment borer, and 6) UTM coordinates, using a handheld base station-correctable GPS unit (March II, Corvallis Microtechnology, Inc., Corvallis, OR). We differentially corrected UTM coordinates using the PC-GPS software (Version 2.50a, Corvallis Microtechnology, Inc., Corvallis, OR). We measured overstory canopy closure using both a concave spherical densiometer and a moosehorn coverscope (Moosehorn CoverScope, Medford, OR). Four densiometer readings of overstory cover, taken approximately 1 m away from the nest tree facing

cardinal directions, and 16 moosehorn readings, taken at the same radius with 22.5° spacing between readings, were averaged for each nest site (Bunnell and Vales, 1990; Cook et al., 1995); all readings were taken by the same observer. Wildlife tree classification, as defined by the British Columbia (BC) Ministry of Forests (British Columbia Ministry of Forests, 1998; Guy and Manning, 1994; Thomas, 1979), was determined for each nest tree. This classification system rated five characteristics of the tree on a relative scale: visual appearance, crown condition, bark retention, wood condition (determined by examining the tree core extracted by the increment borer for decay), and lichen loading. The latter was estimated using the BC Ministry of Forests' Photographic Field Guide (Armleder et al., 1992), which rates lichen (*Bryoria* and *Alectoria* spp.) abundance on the lower 4.5 m of the tree, though we based our evaluation on a generalized overall rating for the entire tree. We used this guide to provide four relative classes of abundance: low (≤ 5 g of lichens per 4.5 m of tree bole), moderate (5–50 g of lichens per 4.5 m), high (50–250 g of lichens per 4.5 m), and very high (250–625 g of lichens per 4.5 m). We also determined a wildlife habitat value (high, medium, or low) for each nest tree, using a combination of species longevity, site position, decay value (based on the visual appearance rating for the wildlife tree classification), diameter (dbh), and tree height (Guy and Manning, 1994).

Habitat characteristics around nest trees were measured during the summer following each winter field season using nested 5.6-m and 10.6-m radius plots (Carey and Johnson, 1995) with the nest tree at the center of each plot. Within the 10.6-m radius plot, we recorded overall tree density (trees with dbh >7.5 cm), live

tree and snag densities, species composition of trees and dominant overstory species, arboreal lichen abundance on each tree (using the same method as for nest trees), the number of witches' brooms and visible cavities, and the number of fallen trees (using two size classes of >7.5 cm diameter and <7.5 cm diameter). In the 5.6-m radius plot, we measured the density and species composition of saplings (>2 m tall, <7.5 cm dbh), understory cover (estimated visually using three classes: 0-10%, 10-50%, 50-100%), and dominant understory, midstory, and herb species. The biogeoclimatic ecosystem classification (Pojar et al., 1987) at each nest site was determined using the BC Ministry of Forests' Field Guide for the Prince Rupert Forest Region (Banner et al., 1993). This classification system is based on the soil moisture and nutrient regime, slope position, and vegetative species composition of the site. In addition, ecosystem mapping, which classifies the area based on seral stage (related to stand structure), seral association (corresponding to successional status), and site units (describing climax potential), had been conducted at the Smithers site (MacKenzie and Banner, 1991). The classification of each mapped unit (polygon) was based on differences in vegetative structure and composition, and on landscape position. Seral stages were reported as shrub-herb, pole/sapling (10–30 years following disturbance), young/mature (young: 30–80 years; mature: 80+ years after stand disturbance), and old-growth (150–250+ year-old stands). Site descriptions of polygons were coded relative to gradients in soil moisture and nutrient regimes, and have since been replaced by the above biogeoclimatic ecosystem classifications. To make both methods directly comparable, we determined an ecosystem type for each site description and biogeoclimatic

ecosystem classification using five moisture and nutrient regimes (dry, mesic, mesic-wet, wet, and forested wetland).

We sampled three random sites for each nest tree. An initial bearing was randomly selected; the other two bearings were 90° and 180° from the first. A distance between 22 and 50 m was randomly selected for each bearing; 22 m was the required minimum to avoid overlapping of plots, and 50 m was set to limit the sampling to an area that we believed to be readily accessible to an animal when selecting its nest site. At each random location, we designated the closest tree (with dbh >7.5 cm) as the 'random nest tree' and the center of the nested plots for that sample. All measurements of tree and habitat characteristics were conducted as for nest trees, with the exception that moosehorn coverscope readings were not taken at 'random nest trees'.

Statistical analyses

An alpha level of 0.05 was assumed for all analyses. Unless otherwise stated, all means are presented as $\bar{X} \pm SE$. Animals located <10 times ($n = 4$) were excluded from calculations of the minimum and maximum distance between nest trees, which were computed using the PC-GPS software (Version 2.50a, Corvallis Microtechnology, Inc., Corvallis, OR), and from calculations of the core nest area. Core nest areas, defined as the area enclosed by an individual's nest trees, were calculated using CALHOME (Kie et al., 1996). We used the 100% utilization distribution of the minimum convex polygon method (Jennrich and Turner, 1969) because this method has the fewest assumptions related to how the area between nest trees was used by the animals. Because the core nest area data were not

normally distributed and could not be successfully transformed, a Wald-Wolfowitz runs test (Siegel, 1956), which includes an adjustment for small sample sizes, was used to test for differences between the distributions of male and female core nest areas. A Levene's test for homogeneity of variances (Milliken and Johnson, 1984) was used to test for differences in the variance between male and female core nest areas. We used correlation analyses (Moore and McCabe, 1993) to examine the relationships between the size of core nest areas and the duration of time that animals were monitored, and with the number of nest trees used per animal. The spatial distribution of nest trees used by aggregating animals and the frequency of nest tree use were visually inspected.

To determine if flying squirrels selected specific structural attributes for nesting, we divided several variables into classes to examine the average percentage of observations per animal in each class. Nest trees were divided into seven dbh classes (in 10-cm increments), seven age classes (in 20-yr intervals), and five height classes (in 10-m increments). We used Student's paired *t*-tests (Moore and McCabe, 1993) to compare each structural attribute (dbh, age, height, and canopy closure) of each nest tree by animal to the average of its randomly sampled trees. We used one-tailed analyses for all attributes except canopy closure because of our hypothesis that flying squirrels select significantly larger, older, taller trees for nesting. To determine the frequency of occurrences in which each animal selected larger, older, or taller trees, we calculated the proportion of nest trees, by animal, that were larger than the average of the associated random samples for each structural attribute. The average proportion across animals was

compared (one-tailed Student's *t*-test) to a null hypothesis of 0.5, which would be expected if nest trees were selected at random with the given attributes having no effect on nest tree selection. Habitat characteristics around nest trees were compared to random locations using analyses similar to those for attributes of the nest tree: paired *t*-tests (two-tailed) and proportional differences. One animal was excluded from these analyses because it used only two nest trees, both of which were shared with another flying squirrel. A paired *t*-test compared densiometer and moosehorn readings at each nest tree. We conducted Pearson Chi-square (χ^2) contingency analysis (Everitt, 1977) on frequency data to determine 1) if the species composition of nest trees deviated from randomly sampled trees by site, and 2) if the biogeoclimatic ecosystem classification differed between nest trees and random sites or between classifications determined on-site at the nest trees and those obtained from polygon descriptions on the ecosystem map of the Smithers Community Forest. Descriptive statistics, *t*-tests, correlations, tests of normality, nonparametric tests, and all graphical representations were completed using STATISTICA (StatSoft, Inc., 1997).

RESULTS

Core nest areas

Nineteen northern flying squirrels (12 males and 7 females) were radiocollared and monitored over the two field seasons. We located the animals 568 times in 82 daytime nest trees. The core nest areas used by flying squirrels averaged 2.74 ± 0.62 ha in size. Males used a wider range of sizes (0.86–8.58 ha)

than females (range = 0.03–2.23 ha), with a significantly higher variance (F = 11.181, *d.f.* = 1,13, P = 0.005). Furthermore, the distribution of core nest areas differed between males and females (*Z-adjusted* = 2.072, P = 0.038; Fig. 1). The size of core nest areas was not correlated with the length of time an animal was monitored (r = 0.28, P = 0.320, n = 15), but was positively correlated with the number of nest trees used by the animal (r = 0.58, P = 0.022, n = 15). When two males, for which core nest areas contained large portions that were not used by the animals (one animal moved to a new area and the other core nest area contained a road), were removed from the analysis, the relationship was even stronger (r = 0.75. P = 0.003, n = 13). The smallest distance between nest trees for each animal averaged 60.1 ± 15.5 m (range = 7.5–203.3 m); the maximum distance between nest trees averaged 361.2 ± 42.7 m, ranging from 78.4 to 751.4 m. The average maximum distance between nest trees was significantly larger for males (435.7 ± 51.1 m) than for females (249.5 ± 48.0 m; t = 2.51, *d.f.* = 13, P = 0.026).

The spatial and temporal use of nest trees varied among individual animals. Some used predominantly one or two nest trees in their core nest areas, whereas others used several trees relatively uniformly throughout the time they were monitored (Fig. 2). The use of individual nest trees ranged from 1.2 to 85.5% of an animal's observations in core nest areas. Overlap occurred when two radiocollared animals used the same nest tree, but at different times. This situation occurred twice: once with a tree used by animals in different years and once during the same winter season. Overlap in core nest areas also occurred in the case of aggregating animals (see Chapter I for descriptions; Fig. 3). In these instances, two or three

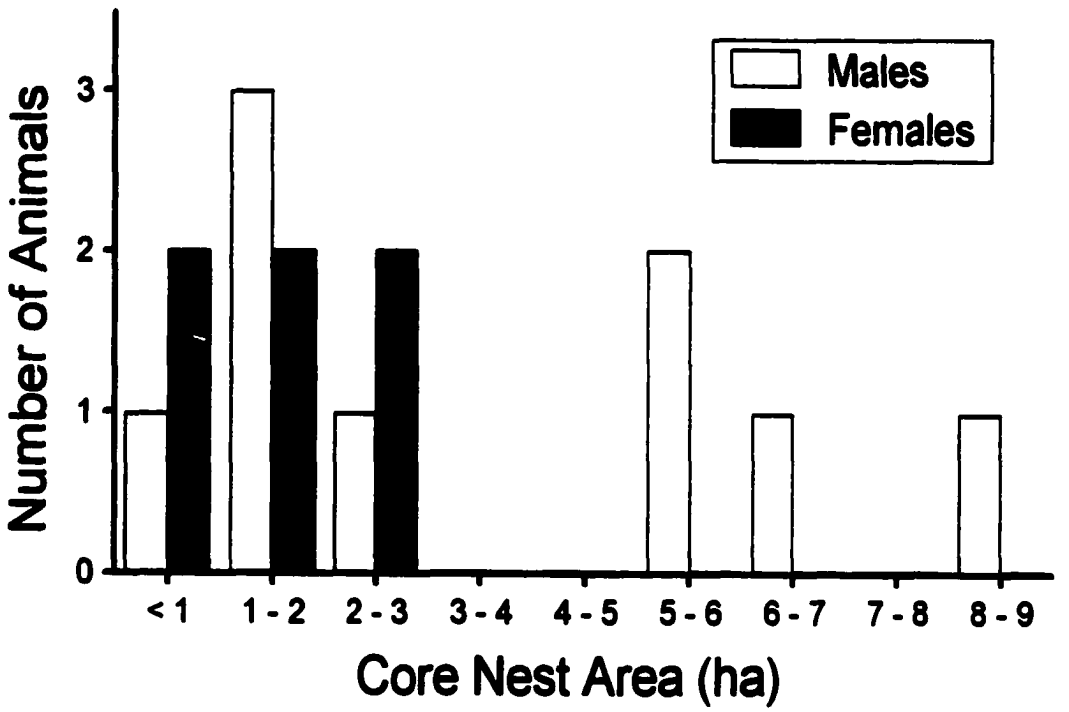

Fig. 1. Distributions in sizes of core nest areas used by nine male and six female northern flying squirrels in northwestern British Columbia.

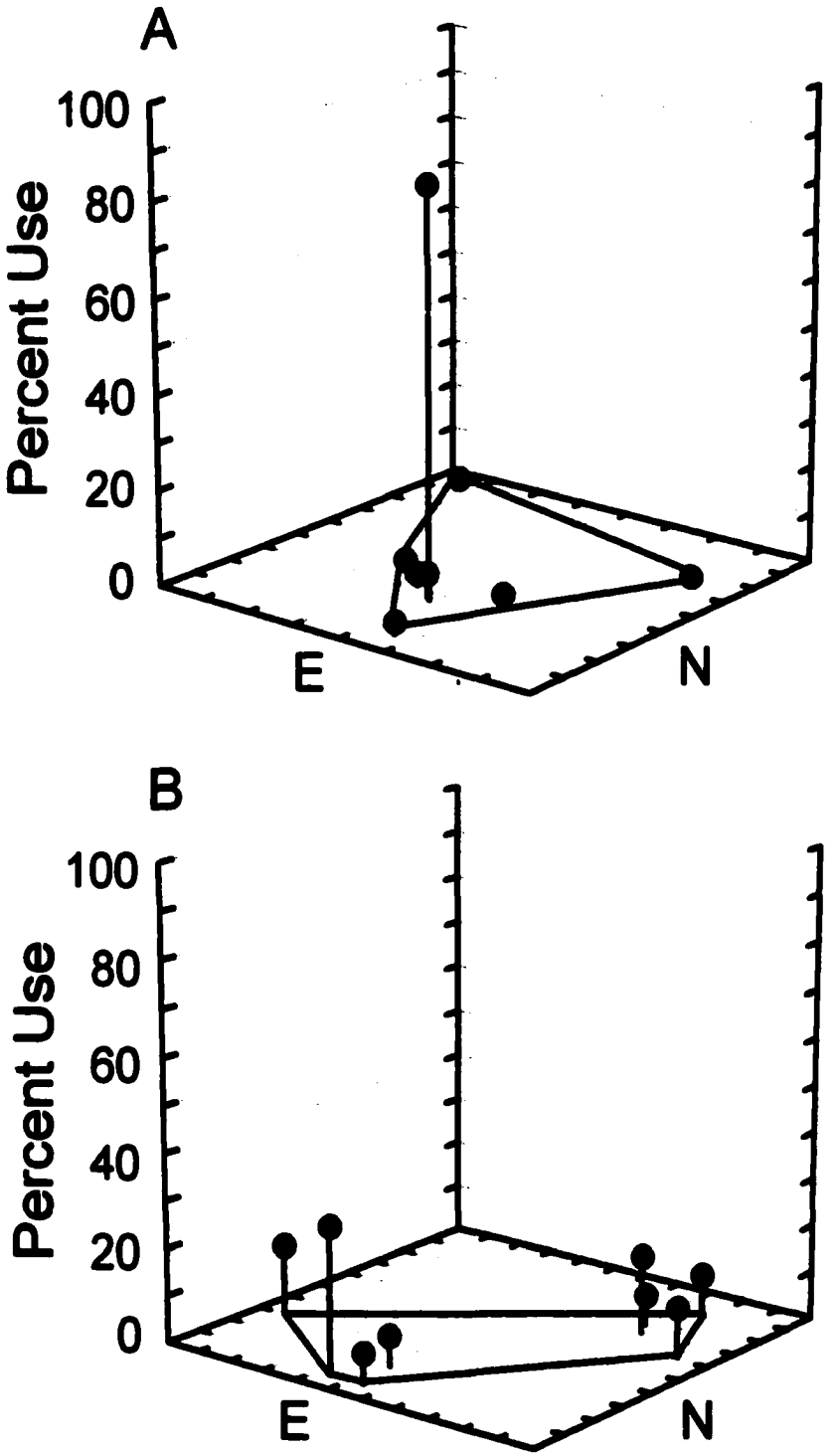

Fig. 2. Examples of the spatial distribution and percent use of nest trees by northern flying squirrels: A) male at the Houston site during 1996 winter (Sep–Mar; eight nest trees; outlined core nest area = 5.09 ha); B) male at the Smithers site in 1997 winter (Sep–Feb; eight nest trees; outlined core nest area = 8.58 ha). Each grid cell in the X-Y plane = 0.25 ha.

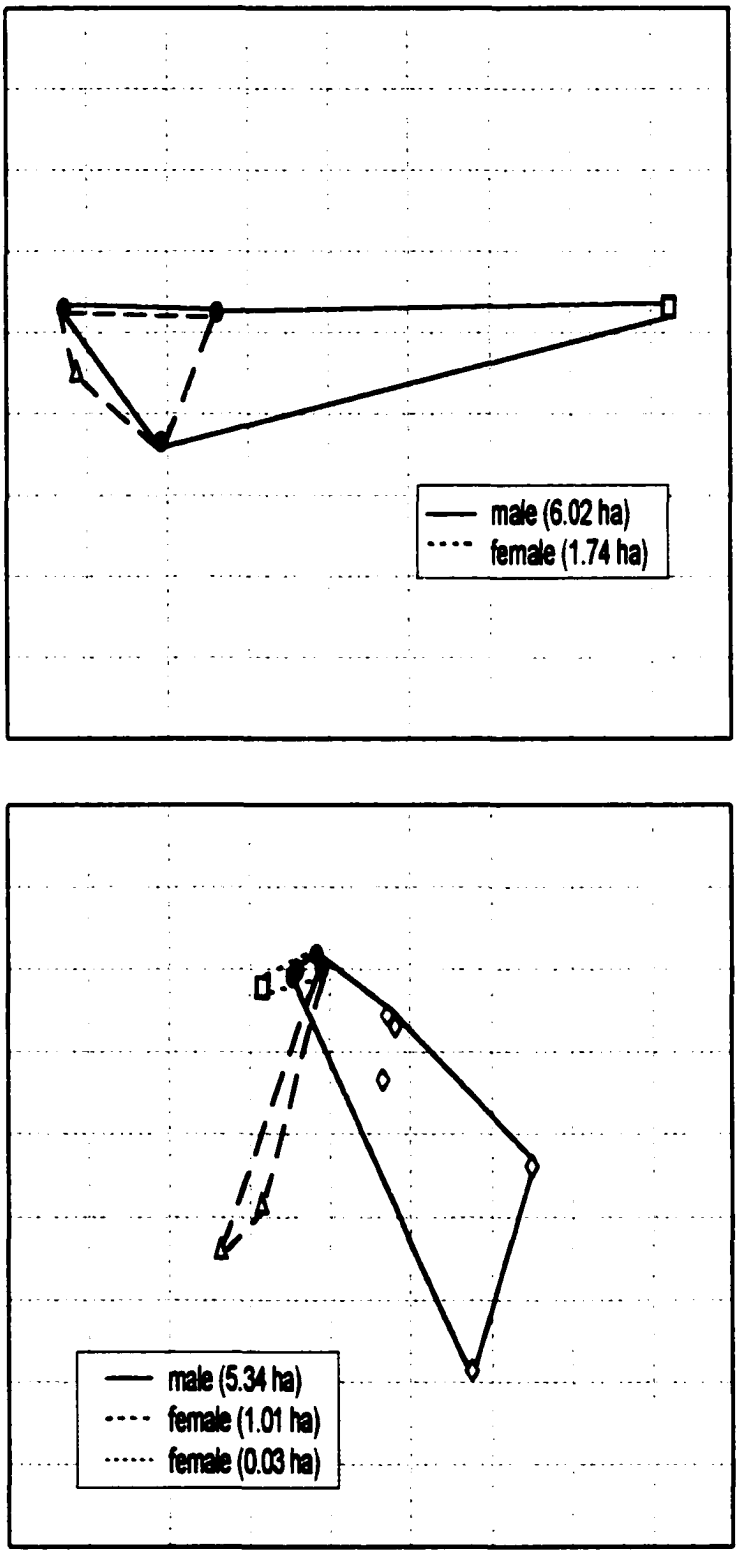

Fig. 3. Examples of overlapping core nest areas of aggregating northern flying squirrels. Symbols indicate nest trees; solid symbols represent nest trees that were used by more than one animal. Each grid cell = 1 ha.

radiocollared animals shared three or four nest trees for extended periods of 1–2 months.

Habitat characteristics

Characteristics of the nest trees were highly variable: dbh ranged from 16.7 to 79.0 cm ($\bar{X} \pm SD = 33.3 \pm 13.3$), age from 42 to 174 years ($\bar{X} = 83.2 \pm 22.7$), and tree height from 11.2 to 32.7 m ($\bar{X} = 22.2 \pm 4.7$). The greatest proportions of the nest trees used by each animal were between 25 and 35 cm dbh, 60 and 80 years, and from 20 to 25 m tall (Fig. 4). Of the 18 animals for which nest tree characteristics were compared with random samples using paired *t*-tests, only four animals selected trees with significantly larger dbh, four selected taller trees, and three selected older trees than the associated 'random nest trees'. However, an inherent problem with the paired *t*-tests (by animal) is that the magnitude of one comparison may have a strong effect on the other comparisons in the set if there is high variation among the values. In the case in which an animal chose a very small nest tree, the large difference between that tree and 'random nest trees' would overwhelm the paired-*t* differences for the animal's other trees, even if those nest trees were larger than the associated 'random nest trees'. Therefore, we examined the proportions of nest trees that were larger, older, or taller to weight each nesting choice equally. When analyzed relative to the frequency of selecting those attributes, a significant proportion of nest trees used by flying squirrels were larger in dbh, age, and height than the average of the associated random samples for each tree (Table 1). Canopy closure was significantly higher at nest trees when recorded with a densiometer ($\bar{X} = 77.4 \pm 1.8\%$; range = 24.2–98.7%) than with a

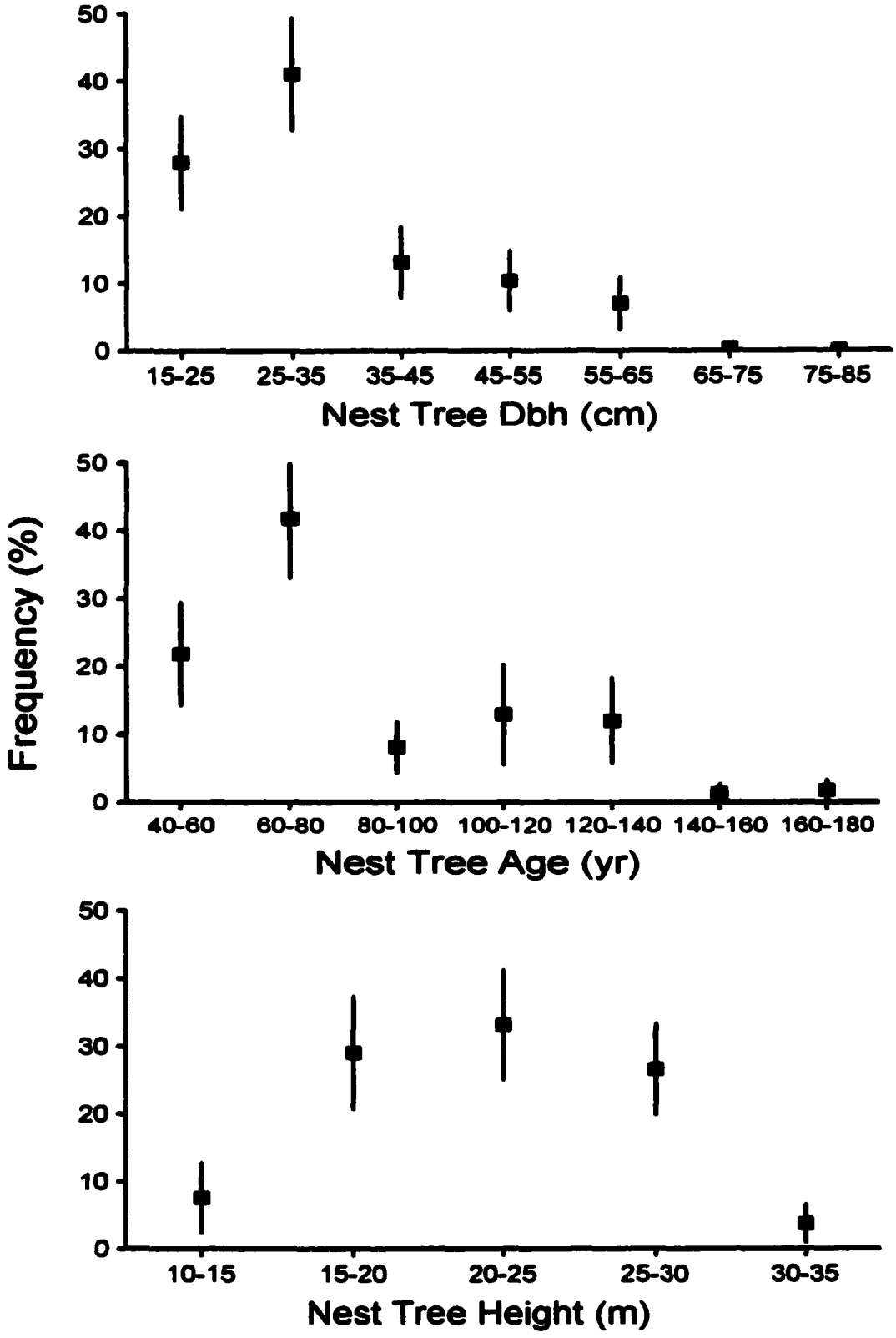

Fig. 4. Relative frequency (averaged across animals; $\bar{X} \pm SE$) of 82 nest trees used by 15 northern flying squirrels by class of tree characteristics.

Table 1. The average proportion (averaged across animals, $n = 18$) of nest trees used by northern flying squirrels in northwestern British Columbia that were larger than the average of the associated random samples for dbh, age, and height (tested against a null hypothesis of 0.5).

Characteristic	Proportion ($\bar{X} \pm SD$)	t_{17}	P
Dbh	0.771 ± 0.188	6.116	< 0.001
Age	0.657 ± 0.273	2.436	0.013
Height	0.756 ± 0.211	5.148	< 0.001

moosehorn coverscope ($\bar{X}$ = 72.2 ± 2.4%; range = 27.5–100%; t = 2.74, $d.f.$ = 81, P = 0.007). Canopy closure at nest sites was not significantly different from random sites.

The wildlife tree classification indicated 91.5% of nest trees had intact crowns, 85.4% of trees had minimal (<5%) bark missing, and 70.7% of trees had relatively sound wood with limited or essentially no decay present, as determined from core samples taken at 1.3 m. Abundance of arboreal lichens (*Bryoria* spp., *Alectoria sarmentosa*) on nest trees was low to moderate (≤50 g of lichens per 4.5 m of tree bole) for 92.7% of the selected trees and similar within nest tree habitat plots and at random sites. Wildlife habitat value, as defined in Guy and Manning (1994), was high for 6.1% of nest trees, medium for 87.8% of nest trees, and low for 6.1% of nest trees (see Appendix B).

The species composition of the nest trees (Table 2) was significantly different from the randomly sampled trees at the Smithers site (*Pearson* χ^2 = 12.741, $d.f.$ = 2, P < 0.002), but not at the Houston site (*Pearson* χ^2 = 1.869, $d.f.$ = 1, P = 0.172). Only three nest trees were snags (one hybrid white spruce, one lodgepole pine, one aspen) and only 14 had visible nests (11 witches' brooms and 2 drays on hybrid white spruce, 1 cavity in a lodgepole pine). Those nests were at an average height of 11.5 ± 1.1 m. All other nesting sites were presumed to be in cavities or nest structures that were not visible from the ground.

The habitat characteristics that we measured in the plots surrounding nest trees were also highly variable (Table 3). When compared with the associated random plots using paired t-tests, only one animal showed a significantly greater

Table 2. Species composition of the nest trees used by northern flying squirrels and of the randomly sampled trees at each study site in northwestern British Columbia.

	% Hybrid white spruce	% Lodgepole pine	% Subalpine fir	% Aspen	% Cottonwood	% Birch
Smithers site:						
nest trees (n = 52)	59.6	26.9	7.7	3.8	1.9	0
random trees (n = 156)	40.5	25.9	32.9	0.6	0	0
Houston site:						
nest trees (n = 30)	66.7	33.3	0	0	0	0
random trees (n = 90)	73.9	19.6	5.4	0	0	1.1

Table 3. Habitat characteristics surrounding 82 nest trees used by 19 northern flying squirrels in northwestern British Columbia.

Habitat Characteristic	$\bar{X} \pm SD$	Range
Tree density (trees/ha)	1234.2 ± 661.0	171.4 – 3428.6
Live tree density (trees/ha)	1044.3 ± 583.5	142.9 – 3257.1
Snag density (trees/ha)	189.9 ± 163.3	0.0 – 714.3
Small fallen trees (<7.5 cm diameter)	650.5 ± 773.3	57.1 – 4428.6
Large fallen trees (>7.5 cm diameter)	437.6 ± 247.2	28.6 – 1457.1
Sapling density (trees/ha)	1003.7 ± 1449.3	0.0 – 7700.0

tree density around its nest trees, one animal showed a greater density of snags although another showed a lower density of snags surrounding nest trees, and two flying squirrels had fewer large fallen trees (>7.5 cm dbh) whereas one animal had fewer small fallen trees in plots around nest trees than in associated random samples. The average proportion of cases in which habitat characteristics surrounding nests were greater than associated random plots did not differ from the null hypothesis, nor did the average proportion of plots that had smaller densities than found in associated random plots. The number of witches' brooms per 353 m^2 plot surrounding nest trees ranged from 0 to 11. Dominant overstory species were generally hybrid white spruce and/or lodgepole pine, with subalpine fir and/or hybrid white spruce as the dominant regenerating midstory species. Dominant understory species included black huckleberry (*Vaccinium membranaceum*), thimbleberry (*Rubus parviflorus*), purple peavine (*Lathyrus nevadensis*), and red-stemmed feathermoss (*Pleurozium schreberi*) (see Appendix C), which are some of the common indicator species in the biogeoclimatic ecosystem classification. Understory cover of herbs and non-woody shrubs was high (>50% cover) for the majority (65.9%) of nest tree plots.

Ecosystem types around nest trees did not differ significantly from random locations at either study site (Table 4). The biogeoclimatic ecosystem classification of nest trees was the same as the associated random samples 64% of the time. Mesic and mesic-to-wet types were most common, with 11 of 18 animals using more than one type of ecosystem. Ecosystem types, as determined from the ecosystem mapping of the Smithers Community Forest, did not always match on-site

Table 4. Comparisons of 1) ecosystem types around nest trees used by northern flying squirrels and their associated random samples and 2) classifications determined for nest trees on-site and from ecosystem maps (MacKenzie and Banner, 1991) at the Smithers site.

	Occurrence of ecosystem type (%)				
	Dry	Mesic	Mesic-Wet	Wet	Forested Wetland
Nest trees (n = 82)	11.0	39.0	30.5	18.3	1.2
Random locations (n = 246)	10.8	39.2	38.0	11.2	0.8
On-site (n = 52)	1.9	42.3	25.0	28.8	1.9
Ecosystem maps (n = 52)	5.8	40.4	38.5	11.5	3.8

determinations (19 of 52 comparisons), but they were not significantly different (Table 4; $\chi^2 = 6.356$, $d.f. = 3$, $P = 0.096$). The map polygons were usually classified as the next most closely related ecosystem type when there was a discrepancy (16 of 19 cases). The distribution of nest trees at the Smithers site by seral stage of the stands (also determined from the ecosystem maps) was as follows: 1.9% in shrub/herb stands, 38.5% in pole/sapling stands, 53.8% in young/mature stands, and 5.8% in old-growth stands. However, 45% of the nest locations in pole/sapling and 7.1% of the locations in young/mature seral stages occurred in four polygons that also contained old veteran trees remaining in the stand after disturbance. Pole/sapling and young/mature stands were the most common stand types in the area, and only a few pockets of old-growth stands were available to animals (see Chapter III). At the Smithers site, 8 of the 12 animals used nest trees in two types of seral stages as determined from the ecosystem maps; the remaining animals used only one type.

DISCUSSION

Core nest areas

Northern flying squirrels occupied core nest areas that were highly variable in size and used a variable number of nest trees. We defined core nest areas for flying squirrels instead of home ranges because our data reflect only nest sites and may not incorporate all foraging areas. Nighttime telemetry efforts to delineate foraging areas were not successful (see Chapter I). Hence, this may contribute to our values of core nest area being smaller than those studies that reported on sizes

of traditional home ranges. Home ranges were similar in Oregon (Martin and Anthony, 1999; Witt, 1992) and West Virginia (Urban, 1988), although sample sizes were low in most areas (Table 5). We observed that the sizes of the core nest areas used by males were more variable than those of females. Males that occupy larger territories may have greater access to females than males with smaller areas (Gerrow, 1996; Martin and Anthony, 1999). Males also showed a larger average maximum distance between nest trees than females. Other studies support a difference in home range sizes between sexes for northern flying squirrels (Gerrow, 1996; Martin and Anthony, 1999) and for closely related southern flying squirrels (Bendel and Gates, 1987).

The spatial and temporal use of nest trees did not follow a consistent seasonal pattern, as might be expected if food became very patchily distributed in winter, leading to larger core nest areas. Instead, animals had individual strategies. Some used many of their nest trees throughout the winter field season while others were extremely faithful to only one or two nests. We observed both strategies in both field seasons. Those strategies may be influenced by social factors that we were unable to measure, such as competition for nest sites by conspecifics and other species (e.g., red squirrels (*Tamiasciurus hudsonicus*)) and the occurrence of aggregations with other flying squirrels. We observed overlap of core nest areas during aggregation and also when nest trees were used by more than one animal without aggregation. Overlap of core nest areas suggests overlap of home ranges. This overlap is not unusual given the diverse habitat characteristics of the area and

Table 5. Size of home ranges reported for northern flying squirrels across North America.

Home range (ha) (range) $\bar{X} \pm SE$	Sex	*n*	Method	Location	Source
3.7 ± 0.9 (0.9–8.6)	males	9	minimum convex polygon[a]	northwestern British Columbia	current study
1.4 ± 0.4 (0.03–2.2)	females	6			
10.3[b] (2.1–14.5)	sexes combined	5	minimum convex polygon[a]	northwestern British Columbia	Mahon and Steventon (1993)
4.2 ± 0.3 (3.4–4.9)	sexes combined	4	minimum convex polygon	western Oregon	Witt (1992)
5.9 ± 0.8 (2.6–17.0)	males	20	adaptive kernel	central Oregon	Martin and Anthony (1999)
3.9 ± 0.4 (1.9–8.0)	females	19			
12.5[c] (2.7–17.0)	males	7	minimum convex polygon	New Brunswick	Gerrow (1996)
2.8[c] (2.2–6.9)	females	8			
5.2 ± 1.1 (3.1–6.8)	males	3	modified minimum area	West Virginia	Urban (1988)

[a] calculated from nest tree locations only, without observations of animal activity
[b] *SD* and/or *SE* not provided
[c] values are medians

the social nature of the animals, as seen by aggregating behaviour (Carey et al., 1997; Mowrey and Zasada, 1984). Gerrow (1996) reported that males and females often foraged together in New Brunswick; females showed very little overlap of home ranges, whereas home ranges of males often overlapped each other and encompassed large parts of smaller female home ranges.

Habitat characteristics

Northern flying squirrels showed considerable flexibility in the characteristics of the nest trees that they selected. Size (dbh and height) and age of nest trees were extremely variable, ranging from 50 to 150% of mean values. None of the animals in our study nested only in the largest nest trees; rather, animals used from 3 to 10 different and highly variable trees. Animals did not have access to large numbers of very large, old trees in the study area; in comparison to trees that were randomly available in the locale of nest trees, however, animals selected a significant proportion of trees that were larger, older and taller. Gerrow (1996), Martin (1994), and Carey et al. (1997) also showed that flying squirrels selected larger nest trees than were available. Our data provide further evidence that flying squirrels are not limited to old-growth habitats as formerly believed, but within younger stands they select large trees from what is available.

The mean values of nest tree characteristics determined in this study are comparable to findings in interior Alaska (Mowrey and Zasada, 1984), central British Columbia (Peterson and Gauthier, 1985), Alberta (McDonald, 1995), and second-growth forests of central Oregon (Martin, 1994), but not to data obtained from the coastal forests of Oregon (Witt, 1992; Carey et al., 1997), where trees were typically

larger, or New Brunswick (Gerrow, 1996), where trees were shorter. In all studies, a wide range of dbh and height was reported for nest trees (Table 6). Given this variation, it appears likely that northern flying squirrels select for trees with suitable nests rather than for tree size. It is probable that potential nest sites (cavities, witches' brooms) are more likely to occur in larger, older trees.

Canopy closure around nest trees also showed high variability. We used two methods to measure canopy closure because of recent studies indicating that spherical densiometers are biased towards overestimating cover (Bunnell and Vales, 1990; Cook et al., 1995). Our results support those findings. The moosehorn coverscope had a limited, more variable projection of overstory cover, whereas we observed smaller standard deviations and consistently larger readings at each nest tree using the spherical densiometer.

The high percentage (96.5%) of live trees used as nest trees differed from the common view of a 'wildlife tree' as a decaying snag. The low percentage of nest trees classified as having high wildlife habitat value (6.1%) occurred because the majority of nest trees were live trees that were of smaller diameter (<50 cm) and height (<20 m) than the highest rated class (Guy and Manning, 1994). The appropriateness of the variables used in this classification system for determining habitat value for northern flying squirrels seems questionable (also see Chapter III). The abundance of lichens on nest trees was not different from random samples, but arboreal lichens (*Bryoria* spp.) were present at every nest site and throughout the stand. Hence, nest site selection by flying squirrels in our study was probably not limited by the availability of arboreal lichens, which are consumed and also used as

Table 6. Dbh and height ($\bar{X} \pm SE$) of nest trees used by northern flying squirrels across North America (range is given when available).

Location of study	Tree type (*n*)	Dbh (cm) (range)	Tree height (m) (range)	Source
Northwestern British Columbia	conifer (79)	31.5 ± 6.1 (16.7-79.0)	19.3 ± 3.7 (11.2-32.7)	current study
	deciduous (3)	33.4 ± 1.5 (19.9-40.5)	22.3 ± 0.5 (13.9-26.4)	
Northwestern British Columbia	conifer (15)	33.7 ± 3.4		Mahon and Steventon (1993)
Interior Alaska[a]	white spruce (32)	32.6 (10.4-56.1)	24.1 (8.5-38.4)	Mowrey and Zasada (1984)
	paper birch (5)	21.9 (18.0-28.2)	12.6 (5.8-17.4)	
	trembling aspen (6)	30.6 (27.2-35.1)	15.6 (13.4-21.3)	
Central BC[b]	nest trees with cavities (6)	30.4 ± 2.9		Peterson and Gauthier (1985)
Central Oregon	second-growth (65)	36.0 ± 1.6		Martin (1994)
	old-growth (43)	101.0 ± 6.1		
Western Oregon	conifer (7)	66.1 ± 9.3 (16-88)	19.9 ± 4.9 (19-40)	Witt (1992)
Western Oregon	second-growth (with thinning)			Carey et al. (1997)
	live (118)	60.1 ± 1.9	37.6 ± 0.8	
	snags (67)	41.6 ± 2.7	11.0 ± 0.9	
	second- growth (with veteran trees)			
	live (186)	49.0 ± 1.4	32.6 ± 0.5	
	snags (86)	63.7 ± 3.6	12.6 ± 0.8	
Alberta[a]	deciduous	36.5	16.6	McDonald (1995)
New Brunswick[a]	conifer (with broom or dray) (55)	28.6 (7.0-57.0)	14.5 (4.0-22.0)	Gerrow (1996)
	conifer and deciduous			
	(woodpecker cavities) (33)	24.5 (11.5-47.0)	7.4 (2.0-21.0)	
	(natural cavities) (42)	29.7 (15.0-69.0)	9.8 (1.6-24.0)	

[a] *SD* and/or *SE* not provided
[b] species breakdown not given

nesting materials (Hayward and Rosentreter, 1994; Maser et al., 1985).

The most common species of trees used for nesting by northern flying squirrels in northwestern British Columbia were hybrid white spruce and lodgepole pine. The main difference in species composition of nest trees at the Smithers site with that of random samples was the low use of subalpine fir. Subalpine fir tends to decay faster than other conifers in the area, making it a likely species for both natural and excavated cavities. The species composition and accompanying seral stages within the study area, however, have been determined largely by the fire disturbance ecology. Spruce and pine are the dominant overstory species, with subalpine fir naturally regenerating as the dominant midstory species. Much of the subalpine fir in the area is not as old or large as the spruce and pine. Consequently, subalpine fir could become more important as a nest tree species as the stands mature.

The use of snags as nest trees was relatively low (3.5%) in our study, which is similar to findings in Oregon (Carey et al., 1997; Martin, 1994). It has been suggested that live trees may be more suitable as nest sites for cavity nesters because of overhead branches providing protection from weather, increased cover and structural complexity for predator avoidance and escape, and because of the longer persistence of live trees compared to snags (Carey et al., 1997). In contrast, McDonald (1995) reported that 59% of the nest trees used by flying squirrels in the mixedwood forests of Alberta were snags. Gerrow (1996) also found that when cavities were used in New Brunswick, the trees were often snags, but nest use was closely linked to availability; cavities were used where abundant and witches'

brooms were inhabited where they were readily available. The low use of snags and brooms as nest sites (13.4%) in our study likely reflects the relatively young age of the stands. Mowrey and Zasada (1984) found northern flying squirrels primarily in witches' brooms in Alaska and stressed the importance of brooms for aggregations of animals. In our study, brooms were used in only two of the nine nest trees in which we observed aggregations of radiocollared animals (see Chapter I). It is unknown whether animals in other brooms were nesting with flying squirrels that were not radiocollared. We elected not to climb nest trees to investigate because Carey et al. (1997) reported that in 10 of 12 climbs to determine nest type, flying squirrels subsequently left the tree and did not return.

The nest trees used by flying squirrels were located in areas with a high degree of tree regeneration (>1000 saplings/ha; Table 3) and numerous fallen trees that provided substantial amounts of coarse woody debris. Flying squirrels, however, did not appear to select particular habitat characteristics at nest sites that differed from random sites. Most other studies have reported similar results (Gerrow, 1996; Martin, 1994; Payne et al., 1989; Rosenberg, 1990; Urban, 1998), although in coastal Oregon, the presence of large snags (>50 cm dbh) was found to be important and in central Oregon, flying squirrels avoided areas with high densities of small snags (Carey et al., 1997; Martin, 1994). In southwestern Oregon, habitats used by flying squirrels had a high degree of decadence (including snags and logs) and complex canopies (Carey et al., 1999). We suggest that the wide range in the habitat attributes observed in this study is further evidence of the flexibility of these animals and an indication of the structural diversity within the

stand. That diversity may be more important than any particular attribute of the stand, and as a characteristic which is reduced in managed forests, should be the focus of further investigation.

Nest trees tended to be in mesic and mesic-to-wet areas. These sites were rich in soil moisture and nutrients and exhibited high species diversity and structural complexity in the shrub and herb layers. Such sites likely produce more mushrooms, a key component in the diet of flying squirrels (Waters and Zabel, 1995). The distance between nest sites and random sites in our study may not have been great enough to reflect the true availability of all ecosystem types at the landscape level. Large polygons, however, often contain pockets of other ecosystem types. We are confident that we could detect the presence of these pockets and did not observe flying squirrels selecting one particular type of ecosystem. Most nest tree locations (>92%) were in pole/sapling or young/mature seral stages, but 21% of the nest trees at the Smithers site were located in four younger stands that were classified as having old veteran trees present and 35% of nest trees were in stands adjacent to old-growth stands or younger stands with veteran trees (see Chapter III). This further supports the conclusion that, although flexible in their nest site selection, flying squirrels seek out areas with larger trees. Ecosystem maps closely approximated actual ecosystem types at the Smithers site.

In summary, northern flying squirrels exhibited a remarkable flexibility in the nest trees they used. The use of many relatively small trees for nest trees suggests that nests may exist in more situations than previously reported and that suitable nest trees are not readily obvious based solely on size and condition of the tree.

Although we could not determine that particular habitat features were selected by flying squirrels relative to nest site location, retaining large structures and structural diversity is likely important for the persistence of this species. Large structures provide nesting habitat and once fallen, provide coarse woody debris, which serves as a site for mushroom growth and cover for animals while foraging on the ground (Harmon et al., 1986). Structural diversity also may be important for animal movements within the stand and for predator avoidance. Future studies should examine the ecological role that flying squirrels play in dispersing fungal spores and lichen fragments in boreal ecosystems. Research on food habits and foraging strategies would help to define the trophic relationship with ectomycorrhizal fungi that assist conifers in obtaining nutrients and water, and enhance growth (Fogel and Trappe, 1978; Harley and Smith, 1983). This ecological link has important implications for the maintenance of forest health, particularly where management operations have simplified stand structure. In addition, this knowledge would help define the interaction and trade-off between high quality food resources, extremely cold temperatures, and structural attributes that ameliorate those extremes for flying squirrels inhabiting northern latitudes.

Chapter III

Conclusions and forest management implications

The northern flying squirrel is a cavity nester found from temperate coastal forests to northern boreal forests of North America (Wells-Gosling and Heaney, 1984). It forages on mushrooms, especially fruiting bodies of ectomycorrhizal fungi (e.g., *Rhizopogon* spp.), and arboreal lichens (e.g., *Bryoria* spp.), and may therefore play an important role in forest health by dispersing spores of mycorrhizal fungi (Laurance and Reynolds, 1984; Maser et al., 1986; Zabel and Waters, 1997). Woody plants are dependent on ectomycorrhizal fungi to enable the absorption of adequate amounts of soil nutrients (Harley and Smith, 1983). Approximately 20% of these fungi have below-ground fruiting bodies (Molina et al., 1992) and are dependent on small mammals for spore dissemination (Fogel and Trappe, 1978). Arboreal lichens are also dependent on movement by small mammals or wind for dispersal (Lesica et al., 1991). Flying squirrels can transport spores of fungi and fragments of lichens, which are also used for nesting materials, throughout their home ranges, allowing the establishment of new colonies and adding new genetic material to existing colonies (Hayward and Rosentreter, 1994; Maser et al., 1986). Flying squirrels are also prey for several owl species (*Strix* spp.) and mammalian predators such as marten (*Martes americana*) and fisher (*Martes pennanti*). This note summarizes two years of research investigating the core nest areas and the characteristics of nest trees used by northern flying squirrels in northwestern British Columbia.

Study area

The study was conducted in the SBSmc2 biogeoclimatic variant (Sub-boreal Spruce, moist, cold subzone), primarily at the Smithers Community Forest, located 10 km west of Smithers, British Columbia. Dominant tree species included hybrid white spruce (*Picea engelmannii x glauca*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and some trembling aspen (*Populus tremuloides*) and cottonwood (*Popuius balsamifera*). The study area experienced fire disturbance in the 1930's and 1940's. It is characterized by pockets of old-growth stands and veteran trees scattered throughout younger forests.

Habitat characteristics

Radiocollared northern flying squirrels (n = 19) used a wide range of tree sizes for nesting, primarily in hybrid white spruce and lodgepole pine. Visible witches' brooms and drays (constructed nests) comprised 18% of the nests located in this study (n = 82); the remaining nests were presumed to be in cavities. The dbh of nest trees ranged from 16.7 to 79.0 cm, age ranged from 42 to 174 yr, and tree height ranged from 11.2 to 32.7 m; the greatest proportions of the nest trees used were between 25 and 35 cm dbh, 60 and 80 years, and from 20 to 25 m tall (see Chapter II and Appendix B). Although flying squirrels did use some small trees, they tended to select the largest trees available to them. Three-quarters of the animals used at least one nest tree with dbh >43 cm in their nest area and more than two-thirds used at least one tree older than 100 yr.

Using wildlife tree and wildlife tree habitat value classifications (British Columbia Ministry of Forests, 1998; Guy and Manning, 1994; Armleder et al., 1992),

we determined that nest trees had moderate lichen abundance and medium habitat value. Most nest trees were smaller than those ranked highest by the wildlife tree habitat value classification; such very large trees (>50 cm dbh) were present but not common throughout the study area. Wildlife habitat value classification also is highest for snags with moderate decay; however, 96% of nest trees used by flying squirrels were in live trees. Hence, these classification systems may not be appropriate for determining potential nest sites for northern flying squirrels in this area. Flying squirrels likely select for suitable nest sites rather than tree size.

Northern flying squirrels used from 3 to 10 nest trees per animal and the sizes of the core nest areas, defined as the area enclosed by an individual's nest trees, ranged from 0.03 to 8.58 ha. Home ranges of the animals are likely larger, including areas that are used for foraging activities outside core nest areas. Nest trees were located predominantly in mesic and mesic–wet sites, although several were situated on the edges of forested wetlands (Fig. 1; Table 1; see also Chapter II for explanations of site units and ecosystem types). Most animals (61%) used more than one type of ecosystem, as determined by biogeoclimatic ecosystem classification (Banner et al., 1993) and all but one animal had nest trees located in more than one polygon type, as described by the ecosystem map of the Smithers site (MacKenzie and Banner, 1991; see Appendix D). Animals occupied nest sites in a range of seral stages (Fig. 2), including pole/sapling and young/mature stands with old veterans (see Chapter II and Appendix D for age definitions and polygon descriptions). Veteran trees in the study area likely augmented the availability of suitable nest sites for secondary cavity nesters such as flying squirrels.

Fig. 1. Distribution of nest trees used by 12 northern flying squirrels at the Smithers Community Forest in relation to ecosystem types (see Table 1). Ecosystem maps were provided by the Prince Rupert Forest Region. Map scale is 1:25,000.

Table 1. Ecosystem types for site units from ecosystem maps and corresponding biogeoclimatic ecosystem classifications.

Ecosystem type	Site units from ecosystem mapping (MacKenzie and Banner, 1991)	Biogeoclimatic ecosystem classification (Banner et al., 1993)
Dry	Dry Pine (DP)	Lodgepole Pine–Huckleberry–Cladonia (mc2/02)
Mesic	Huckleberry–Moss (HM)	Hybrid White Spruce–Huckleberry (mc2/01)
Mesic–wet	Thimbleberry–Oak fern (TO)	Hybrid White Spruce–Twinberry–Coltsfoot (mc2/05), Hybrid White Spruce–Oak fern (mc2/06)
Wet	Horsetail Flat (HF), Devil's club (DC)	Hybrid White Spruce–Horsetail (mc2/10), Hybrid White Spruce–Devil's club (mc2/09)
Very wet	Forested Wetland (FW) Cottonwood–Cow-parsnip (CC)	Black Spruce–Hybrid White Spruce–Scrub birch–Sedge (mc2/12)
Other	Non-Forested Wetland (NW) Lake (L) Cleared Areas (C)	Non-forested fen/marsh (mc2/31)

Fig. 2 Distribution of nest trees used by 12 flying squirrels at the Smithers Community Forest in relation to seral stage. Ecosystem maps were provided by the Prince Rupert Forest Region. Map scale is 1:25,000.

Management implications

Even-aged management on commercial rotations tends to reduce many of the structural features, such as large diameter trees, snags, and live trees with cavities, necessary for wildlife tree dependent species. New harvesting regimes such as patch retention may be able to provide more suitable habitat for these species by maintaining structural diversity within stands (Coates and Steventon, 1995; Hunter, 1995). Patch retention harvesting typically retains 5–20% of the forested area of a cutblock. Leaving large old trees, both live and dead, provides potential nesting structures once the surrounding stand has regenerated; coarse woody debris left on the ground provides a substrate for forage production, including mushrooms and truffles. The Smithers Community Forest had similar patches of remnant trees left after fire disturbance earlier in the century. Flying squirrels in our study were able to colonize relatively young stands that had large veteran trees present.

In designating patches of trees to be left on the landscape, particular attention should be given to retaining nesting structures, such as large snags, large live trees with cavities, and trees with witches' brooms. The creation of cavities in live trees may be a useful method to ensure that there are adequate numbers of cavities in retained forest patches (Carey and Sanderson, 1981). The amount of interspecific competition for nest sites (e.g., between red squirrels (*Tamiasciurus hudsonicus*) and northern flying squirrels) is not well studied in boreal forests and should be addressed. In the southern extent of its range, the northern flying squirrel is known to be displaced from tree cavities by the smaller, closely related southern

flying squirrel (*Glaucomys volans*) where the two species overlap (Weigl, 1978). Attention should also be given to the location of retained patches. Retention patches are often located in riparian areas. Although some flying squirrels in this study inhabited wet sites, not all animals used riparian zones and retention patches should not be limited to those areas.

Immediately after timber harvest, retention patches may not be large enough to sustain flying squirrels until the surrounding stand has reached a suitable age for travel and foraging. Flying squirrels are highly arboreal and are not likely to cross large openings that would require travel on the ground (Mowrey and Zasada, 1984). Flying squirrels recolonizing remnant patches after surrounding stands have regenerated, however, could potentially assist in the rebuilding of the mycorrhizal community in the cut area, as well as transport lichen fragments to the younger stand (Fogel and Trappe, 1978; Lesica et al., 1991). Sufficient mature forest, however, must remain in the landscape to sustain a population and provide for dispersal. Partial cutting, such as single tree selection and patch removal, may be useful in landscapes that are highly fragmented from timber harvesting. Future studies should quantify the role that flying squirrels play in the maintenance of forest health by dispersing mycorrhizal fungal spores and arboreal lichen fragments in boreal forests and the potential benefits of squirrel activity for regenerating northern forests.

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Appendix A. Biological information for northern flying squirrels radiocollared in northwestern British Columbia.

Date	Site	Sex	Weight (g)	Ear tag numbers	Collar frequency (MHz)	Status	Date of last live location	Probable cause of death or loss of signal[a]
9/9/96	Smithers	M	140	L82/R231	149.619	loss of signal	12/4/96	unknown
9/10/96	Smithers	F	150	L232/R233	149.581	loss of signal	11/20/96	unknown[b]
9/13/96	Smithers	M	140	—	149.599	dead	11/20/96	unknown[c]
9/14/96	Houston	M	153	L244/R450	149.459	dead	1/20/97	predator; collar recovered
9/14/96	Houston	M	143	L249/R248	149.559	loss of signal	2/3/97	unknown
9/18/96	Houston	M	148	L449/R250	149.440	loss of signal	12/20/96	unknown
9/20/96	Houston	M	140	L422/R423	149.399	loss of signal	2/27/97	unknown
9/21/96	Houston	F	155	R447	149.359	dead	11/26/96	predator[d]
9/30/96	Smithers	F	130	L420/R457	149.379	loss of signal	12/11/96	unknown
10/2/96	Houston	M	175	L421/R408	149.339	collar removed	3/6/97	released in good health[e]
10/5/96	Houston	F	140	L404/R410	149.318	dead	11/24/96	predator; collar recovered
10/11/96	Smithers	M	139	L403/R417	149.258	loss of signal	11/21/96	unknown
8/14/97	Smithers	F	147	L548/R509	150.450	loss of signal	11/20/97	unknown
9/12/97	Smithers	M	145	L497	150.142	loss of signal	3/4/98	unknown
9/12/97	Smithers	M	148	L406/R499	150.166	loss of signal	2/24/98	unknown
9/13/97	Smithers	F	157	L583/R492	150.124	loss of signal	3/13/98	unknown
9/16/97	Smithers	M	129	L490	150.086	loss of signal	3/4/98	unknown
9/18/97	Smithers	M	135	L476/R477	150.025	loss of signal	3/6/98	unknown
9/22/97	Smithers	F	140	L409	150.519	loss of signal	4/9/98	unknown

[a] Unknown causes related to loss of signal may have been due to collar failure or predation which resulted in the animal and collar being moved beyond our range of detecting the radio signal (e.g., predation by owls). Both recovered collars were found on the ground and showed signs of chewing but were otherwise intact.

[b] Signal was tracked to one of the animal's habitually used nest trees, although collar temperature was calculated to be 4.6°C. Continuous data-logger monitoring for 48 h showed that the signal did not leave the tree. Animal may have died in the tree or collar may have been removed and discarded in nest.

[c] Signal was tracked to a tree never before used by the animal. Collar temperature was -2.4°C and the signal did not leave the tree for 48 h.

Appendix A (cont'd.)

[d] Signal was tracked to a marten den; collar temperature was 5.3°C.
[•] Animal was retrapped at the end of the field season and the collar was removed. Animal weighed the same as at the time of collaring in the fall and showed no signs of chafing or scabbing around its neck. Fecal samples collected during the winter retrapping of the animal were compared with fall samples by crushing one or two pellets that had been stored in 90% ethanol to produce a fecal solution. Several drops of each solution were placed on slides and examined under a compound microscope for the presence of spores. Both samples contained spores, although the fall sample mainly consisted of spores while the winter sample contained predominately other vegetative matter. A method for examining fecal samples systematically and preparing permanent slides is given in Waters and Zabel (1995).

Appendix B. Attributes of 82 nest trees used by 19 radiocollared northern flying squirrels in northwestern British Columbia.

Squirrel collar frequency[a]	Nest tree #	Site	Tree species[b]	Dbh (cm)	Age[c] (yr)	Tree height (m)	Nest type	Nest aspect (°)	Nest height (m)	Wildlife tree class[d]	Wildlife tree habitat value[e]
149.258	33	Smithers	pine	50.8	98	29.0				11232	2
149.258	34	Smithers	pine	29.9	85	22.4				11122	2
149.258	42	Smithers	pine	30.6	64	18.2				23122	2
149.379	55	Smithers	aspen	19.9	*	17.5				44550	2
149.581	1	Smithers	fir	24.8	60	20.7				11141	2
149.581	20	Smithers	spruce	55.7	61	28.5				11231	2
149.581	22	Smithers	pine	41.7	71	25.4				11121	2
149.581	31	Smithers	cottonwood	40.5	52	26.4				11140	2
149.599	6	Smithers	spruce	31.7	78	20.0				11121	2
149.619	23	Smithers	spruce	19.1	55	21.0	broom	303	3.5	11141	2
149.619	2	Smithers	spruce	25.9	56	18.7				11131	2
149.619	7	Smithers	spruce	44.8	174	31.4				11131	2
149.619	12	Smithers	spruce	48	103	32.7				11341	2
149.619	41	Smithers	spruce	59.9	87	29.7				11121	1
149.619	48	Smithers	pine	25.8	76	25.7				12111	2
150.025	26A	Smithers	spruce	52.5	172	24.8				11311	1
150.025	29A	Smithers	spruce	31.4	115	19.5				11131	2
150.025	7A	Smithers	spruce	33.8	73	19.2				11121	2
150.086	16A	Smithers	spruce	29.6	77	17.3				11111	2
150.086	21A	Smithers	spruce	49.2	90	27.1				11121	2
150.086	28A	Smithers	pine	27	81	24.7				11112	2
150.086	50A	Smithers	spruce	27.1	90	21.0				11111	2
150.086	5A	Smithers	spruce	40.7	136	24.4				11341	2
150.124	14A	Smithers	spruce	19.7	140	12.0				11222	2
150.124	3A	Smithers	spruce	20.4	84	16.6				11131	2

Appendix B (cont'd.)

Squirrel collar frequency[a]	Nest tree #	Site	Tree species[b]	Dbh (cm)	Age[c] (yr)	Tree height (m)	Nest type	Nest aspect (°)	Nest height (m)	Wildlife tree class[d]	Wildlife tree habitat value[e]
150.142	55A	Smithers	spruce	55.8	95	26.3	broom	105	11.4	11121	2
150.142	20A	Smithers	spruce	28.4	76	17.5	broom	315	11.4	11121	2
150.142	25A	Smithers	spruce	69.8	84	27.0	broom	120	14.7	11241	2
150.142	11A	Smithers	spruce	24.7	106	20.2				11121	2
150.142	24A	Smithers	fir	29.3	80	19.7				11141	3
150.142	27A	Smithers	spruce	28.2	73	20.6				11121	2
150.142	2A	Smithers	pine	29.3	85	20.9				11131	2
150.166	9A	Smithers	spruce	24.2	69	22.9	broom	75	14.6	11121	2
150.166	4A	Smithers	pine	52.7	94	25.0				11141	1
150.166	6A	Smithers	pine	40.2	77	27.9	cavity	30	13.6	11122	2
150.166	12A	Smithers	pine	53.9	81	26.3				12123	2
150.166	17A	Smithers	pine	23.8	47	17.6				11121	2
150.166	23A	Smithers	spruce	79	105	32.0				11221	2
150.450	10A	Smithers	spruce	21	54	15.1	dray	264	6.2	11131	2
150.450	13A	Smithers	fir	20.75	69	15.3				11121	3
150.450	19A	Smithers	spruce	22.4	79	17.3				11121	2
150.450	1A	Smithers	spruce	46.5	60	17.6				11211	2
150.519	51A	Smithers	spruce	35	148	20.5	broom	22	11.5	22353	2
150.519	8A	Smithers	spruce	16.7	53	11.2	broom	291	6.3	11121	2
150.519	15A	Smithers	aspen	34.1	*	13.9				11350	2
150.519	30A	Smithers	spruce	36.7	71	21.5				11111	2
150.519	31A	Smithers	fir	26.2	132	19.2				11111	2
149.379, 149.599	25	Smithers	pine	21.6	62	19.9				11121	2
149.379, 149.599	32	Smithers	spruce	24.7	58	19.3				11121	2

Appendix B (cont'd.)

Squirrel collar frequency[a]	Nest tree #	Site	Tree species[b]	Dbh (cm)	Age[c] (yr)	Tree height (m)	Nest type	Nest aspect (°)	Nest height (m)	Wildlife tree class[d]	Wildlife tree habitat value[e]
149.379, 149.599	45	Smithers	pine	31.1	77	25.5				11141	2
149.619, 150.124	14	Smithers	pine	43.4	78	25.0				11132	2
150.086, 150.142	18A	Smithers	spruce	62.7	99	27.9				11141	1
149.318	30	Houston	pine	18.4	48	28.5				11112	2
149.318	40	Houston	spruce	49.7	54	25.9				11252	2
149.339	58	Houston	spruce	20.6	57	20.0	broom	141	10.8	11111	2
149.339	56	Houston	spruce	27.6	59	23.6	dray	253	15.4	11222	2
149.339	29	Houston	spruce	28.2	71	17.7				11132	2
149.339	39	Houston	spruce	20	49	16.7				11122	2
149.339	54	Houston	spruce	47.5	100	29.4				11442	2
149.339	57	Houston	pine	23.2	49	20.4				11113	2
149.359	16	Houston	spruce	54.9	123	27.7				11341	2
149.359	52	Houston	spruce	19.1	47	18.1				11212	3
149.399	13	Houston	pine	28.6	109	23.8				11122	2
149.399	15	Houston	pine	33	113	25.8				11211	2
149.399	24	Houston	pine	28.8	100	27.3				11262	2
149.399	26	Houston	pine	28.7	87	19.6				11243	3
149.399	35	Houston	pine	19.2	69	17.0				33441	2
149.399	37	Houston	pine	26.5	115	24.5				11162	2
149.399	47	Houston	pine	24.2	122	23.1				11123	2
149.399	50	Houston	pine	25.6	100	24.8				11162	2
149.420	11	Houston	spruce	27.5	100	23.3	broom	52	18.6	32561	1
149.459	8	Houston	spruce	31.8	57	19.5				11121	2
149.459	21	Houston	spruce	29	48	23.8				11341	2

Appendix B (cont'd.)

Squirrel collar frequency[a]	Nest tree #	Site	Tree species[b]	Dbh (cm)	Age[c] (yr)	Tree height (m)	Nest type	Nest aspect (°)	Nest height (m)	Wildlife tree class[d]	Wildlife tree habitat value[e]
149.459	44	Houston	spruce	37.5	51	21.9				11231	2
149.559	10	Houston	spruce	18.6	62	18.3				11151	2
149.559	17	Houston	spruce	24.8	76	18.8				11231	2
149.318, 149.339, 149.359	38	Houston	spruce	18.6	42	17.5	broom	238	12.84	11122	3
149.339, 149.359	46	Houston	spruce	25.8	63	21.8				11113	2
149.339, 149.359	49	Houston	spruce	19.9	57	17.7				11212	2
149.339, 149.359	51	Houston	spruce	22.5	58	20.0	broom	63	10.63	11122	2
149.440, 149.559	53	Houston	spruce	44.6	139	29.8				11321	2
149.440, 149.559	28	Houston	spruce	43.5	137	28.8				11221	2

[a] More than one collar frequency per nest tree, as denoted by commas, indicates that each of the animals used the nest tree.

[b] Tree species included lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), hybrid white spruce (*Picea glauca x engelmannii*), trembling aspen (*Populus tremuloides*), and black cottonwood (*Populus balsamifera*).

[c] * denotes core of tree too decayed to determine age.

[d] Wildlife tree class is comprised of five digits, each representing a separate variable which was rated on a relative scale: 1st digit = visual appearance; 2nd digit = crown condition; 3rd digit = presence of bark; 4th digit = wood condition; 5th digit = lichen loading (see Chapter II).

[e] Wildlife tree habitat value was determined using the protocol given in Chapter II. 1 = high value; 2 = medium value, and 3 = low value.

Appendix C. Habitat characteristics surrounding 82 nest trees used by 19 radiocollared flying squirrels in northwestern British Columbia.

Squirrel collar frequency[a]	Nest tree #	Site	BEC	Site position	tree density (/ha)	live trees (/ha)	snags (/ha)	sapling density[b] (/ha)	small fallen trees[c] (/ha)	large fallen trees[d] (/ha)	under-story cover[e]	dominant understory species[f]	dominant midstory species[f]
149.258	33	Smithers	mc2/01	top	457.1	285.7	171.4	200	171.4	628.6	2	7,8,9	5
149.258	34	Smithers	mc2/01	mid	1142.9	1000.0	142.9	300	257.1	285.7	2	7,8,10	3,5
149.258	42	Smithers	mc2/01	mid	1428.6	1142.9	285.7	1000	257.1	514.3	2	7,10	1,3
149.379	55	Smithers	mc2/06	flat	1000.0	857.1	142.9	400	571.4	742.9	2	8,13	3,5
149.581	1	Smithers	mc2/06	mid	657.1	571.4	85.7	100	200.0	171.4	3	8,13,40	1,3,5
149.581	20	Smithers	mc2/05	mid	171.4	142.9	28.6	300	142.9	285.7	3	13,14	1,5
149.581	22	Smithers	mc2/06	mid	1400.0	1142.9	257.1	900	228.6	428.6	3	13	1,3,5
149.581	31	Smithers	mc2/05	flat	800.0	714.3	85.7	600	142.9	57.1	2	14,23	1,3
149.599	6	Smithers	mc2/10	flat	971.4	857.1	114.3	100	171.4	426.6	3	32	1,5
149.619	2	Smithers	mc2/10/05	mid	800.0	742.9	57.1	400	114.3	342.9	3	32/14,22	1,3
149.619	7	Smithers	mc2/10	flat	1314.3	942.9	371.4	1100	285.7	514.3	3	9,13,32	1,3,5
149.619	12	Smithers	mc2/06	mid	685.7	571.4	114.3	100	400.0	257.1	2	9,13	1,3,5
149.619	23	Smithers	mc2/06/10	flat	600.0	571.4	28.6	200	228.6	200.0	3	13,15,32	1,3,5
149.619	41	Smithers	mc2/10	flat	342.9	342.9	0.0	100	57.1	114.3	3	20,32	1,3,5
149.619	48	Smithers	mc2/01	mid	1228.6	771.4	457.1	300	314.3	714.3	3	10,13,38	1,3,5
150.025	26A	Smithers	mc2/10	flat	657.1	514.3	142.9	100	57.1	342.9	3	32	5
150.025	29A	Smithers	mc2/10	flat	971.4	800.0	171.4	100	457.1	571.5	3	8,23	5,6
150.025	7A	Smithers	mc2/10	flat	914.3	857.1	57.1	800	85.7	57.1	3	32	5,6
150.086	16A	Smithers	mc2/01	mid	1885.7	1742.9	142.9	1000	828.6	142.9	2	8,10	1,3
150.086	21A	Smithers	mc2/06	mid	1228.6	1142.9	85.7	1400	714.3	514.3	3	8,10	3,5
150.086	28A	Smithers	mc2/01/06	mid	1857.1	1571.4	285.7	600	371.4	600.0	3	9,10,16	1,3
150.086	50A	Smithers	mc2/10	mid	2257.1	1685.7	571.4	500	971.4	342.9	3	32	3
150.086	5A	Smithers	mc2/10	flat	1142.9	1000.0	142.9	600	1228.6	514.3	3	8,32	1,5,6
150.124	14A	Smithers	mc2/10	flat	1285.7	1142.9	142.9	500	971.4	342.9	3	8,13,33	1,5
150.124	3A	Smithers	mc2/10	flat	1285.7	1228.6	57.1	100	542.9	85.7	3	32,33	5
150.142	11A	Smithers	mc2/10	flat	1371.4	914.3	457.1	300	571.4	285.7	3	32,8	3,5
150.142	20A	Smithers	mc2/01	mid	1257.1	1028.6	228.6	0	457.1	428.6	3	8,9,10	3,5
150.142	24A	Smithers	mc2/01	mid	1514.3	1342.9	171.4	700	942.9	142.9	2	8,10	3

Appendix C (cont'd.)

Squirrel collar frequency[a]	Nest tree #	Site	BEC	Site position	tree density (/ha)	live trees (/ha)	snags (/ha)	sapling density[b] (/ha)	small fallen trees[c] (/ha)	large fallen trees[d] (/ha)	under-story cover[e]	dominant understory species[f]	dominant midstory species[f]
150.142	25A	Smithers	mc2/06	mid	2000.0	1685.7	314.3	1300	828.6	371.4	3	10,13	3
150.142	27A	Smithers	mc2/01	mid	3142.9	2942.9	200.0	3500	800.0	228.6	2	8,9	3
150.142	2A	Smithers	mc2/10	mid	1371.4	1114.3	257.1	800	1142.9	857.1	3	32	3,5
150.142	55A	Smithers	mc2/01	mid	1828.6	1485.7	342.9	2000	542.9	914.3	2	9,41	3,5
150.166	12A	Smithers	mc2/01	top	485.7	457.1	28.6	200	371.4	428.6	2	7,16	3,5
150.166	17A	Smithers	mc2/01	mid	2142.9	1828.6	314.3	900	942.9	285.7	3	7,8,9	3
150.166	23A	Smithers	mc2/01	mid	485.7	428.6	57.1	100	200.0	342.9	3	16,42	3,5,6
150.166	4A	Smithers	mc2/01	mid	2057.1	1514.3	542.9	900	685.7	485.7	3	7,9	3,5
150.166	6A	Smithers	mc2/01	mid	628.6	542.9	85.7	600	171.4	600.0	3	7,9,41	3,5
150.166	9A	Smithers	mc2/01	mid	1628.6	1200.0	428.6	500	400.0	571.4	3	7,35	3,5
150.450	10A	Smithers	mc2/01	mid	3428.6	3257.1	171.4	7700	657.1	28.6	2	9,10	3
150.450	13A	Smithers	mc2/01	mid	742.9	685.7	57.1	100	200.0	114.3	2	49	3,5
150.450	19A	Smithers	mc2/01	mid	885.7	771.4	114.3	2800	457.1	285.7	2	8,16,44	3,5
150.450	1A	Smithers	mc2/01	mid	857.1	742.9	114.3	500	171.4	57.1	2	20,41	3,5
150.519	15A	Smithers	mc2/01	mid	3085.7	2771.4	314.3	6600	2057.1	600.0	1	8	1,3
150.519	30A	Smithers	mc2/06	mid	1114.3	1057.1	57.1	1300	571.4	257.1	3	13,20	1,3
150.519	31A	Smithers	mc2/06	flat	1571.4	1000.0	571.4	600	600.0	685.7	3	8,10,13	3
150.519	51A	Smithers	mc2/12	flat	428.6	142.9	285.7	0	257.1	628.6	3	33,46	5,6
150.519	8A	Smithers	mc2/10	mid	2457.1	2285.7	171.4	1700	1600.0	400.0	3	8,10,32	1,3
149.379, 149.599	25	Smithers	mc2/01	flat	2142.9	1828.6	314.3	2500	857.1	600.0	1	8,21	1,3
149.379, 149.599	32	Smithers	mc2/02	mid	1114.3	885.7	228.6	400	857.1	457.1	2	16,26	1,3
149.379, 149.599	45	Smithers	mc2/01	flat	1085.7	942.9	142.9	1200	857.1	371.4	2	7,8,9	1,3
149.619, 150.124	14	Smithers	mc2/06	mid	571.4	542.9	28.6	100	342.9	285.7	3	9,13,14	1,3
150.086, 150.142	18A	Smithers	mc2/01/05	mid	1771.4	1514.3	257.1	3400	2657.1	828.6	2	8,9,14,21	3
149.318	30	Houston	dk/06	top	1742.9	1485.7	257.1	100	771.4	400.0	3	8,11,12	1

Appendix C (cont'd.)

Squirrel collar frequency[a]	Nest tree #	Site	BEC	Site position	tree density (/ha)	live trees (/ha)	snags (/ha)	sapling density[b] (/ha)	small fallen trees[c] (/ha)	large fallen trees[d] (/ha)	under-story cover[e]	dominant understory species[f]	dominant midstory species[f]
149.318	40	Houston	dk/01	flat	600.0	542.9	57.1	100	514.3	285.7	3	5,23	1,5
149.339	29	Houston	dk/06	mid	1000.0	885.7	114.3	100	285.7	371.4	3	14	1
149.339	39	Houston	dk/06	mid	1000.0	885.7	114.3	100	285.7	371.4	3	14	1
149.339	54	Houston	dk/01	mid	1257.1	828.6	428.6	900	1114.3	714.3	2	9,13	1
149.339	56	Houston	dk/01	mid	1428.6	1000.0	428.6	300	514.3	542.9	2	9,23	1
149.339	57	Houston	dk/03	mid	828.6	742.9	65.7	100	285.7	342.9	3	8,24	1,4
149.339	58	Houston	dk/01	mid	1000.0	857.1	142.9	500	885.7	428.6	3	12,14	1
149.359	16	Houston	dk/06	mid	657.1	657.1	0.0	800	342.9	200.0	2	11,12	1,5
149.359	52	Houston	dk/01	mid	1371.4	1342.9	28.6	200	228.6	314.3	3	12,23	1
149.399	13	Houston	dk/03	flat	828.6	800.0	28.6	700	314.3	371.4	3	25	1,2
149.399	15	Houston	dk/01	flat	685.7	685.7	0.0	900	85.7	514.3	3	17,24	1,2
149.399	24	Houston	dk/03	flat	600.0	514.3	85.7	100	142.9	371.4	2	11,24	1,2
149.399	26	Houston	dk/03	top	1057.1	971.4	85.7	4600	457.1	400.0	3	8,29	1,2,5
149.399	35	Houston	dk/03	flat	1000.0	657.1	342.9	600	171.4	657.1	2	16,24	1,2,3
149.399	37	Houston	dk/03	flat	914.3	714.3	200.0	800	171.4	314.3	3	24,25	1,2,6
149.399	47	Houston	dk/03	flat	914.3	714.3	200.0	800	171.4	314.3	3	24,25	1,2,6
149.399	50	Houston	dk/03	flat	914.3	714.3	200.0	800	171.4	314.3	3	24,25	1,2,6
149.420	11	Houston	mc2/01	mid	2000.0	1571.4	428.6	1300	2971.4	1257.1	3	8,9	1,3,6
149.459	8	Houston	mc2/06	mid	1400.0	1257.1	142.9	100	600.0	657.1	3	13,14	3,46
149.459	21	Houston	mc2/06	mid	2171.4	1457.1	714.3	2200	3685.7	1457.1	3	13,14	1,3
149.459	44	Houston	mc2/06	mid	371.4	342.9	28.6	200	257.1	457.1	3	8,13,34	5,6
149.559	10	Houston	mc2/05/06	mid	2200.0	1542.9	657.1	6700	4428.6	600.0	2	8,13,21	1,3
149.559	17	Houston	mc2/01	mid	2400.0	2228.6	171.4	1200	2428.6	685.7	3	8,9	1
149.318, 149.339, 149.359	38	Houston	dk/06	mid	942.9	857.1	85.7	800	400.0	371.4	2	11	1
149.339, 149.359	46	Houston	dk/06	mid	742.9	714.3	28.6	700	428.6	400.0	3	11	1,3
149.339, 149.359	49	Houston	dk/01	mid	1314.3	1285.7	28.6	400	314.3	342.9	2	12,14	1

Appendix C (cont'd.)

Squirrel collar frequency[a]	Nest tree #	Site	BEC	Site position	tree density (/ha)	live trees (/ha)	snags (/ha)	sapling density[b] (/ha)	small fallen trees[c] (/ha)	large fallen trees[d] (/ha)	under-story cover[e]	dominant understory species[f]	dominant midstory species[f]
149.339, 149.359	51	Houston	dk/01	mid	1057.1	1057.1	0.0	200	228.6	285.7	3	9,12	1
149.440, 149.559	28	Houston	mc2/06	mid	542.9	514.3	28.6	1900	371.4	542.9	3	9,14,32	1,5,6
149.440, 149.559	53	Houston	mc2/06	mid	600.0	542.9	57.1	1600	342.9	857.1	3	13,19	1,5

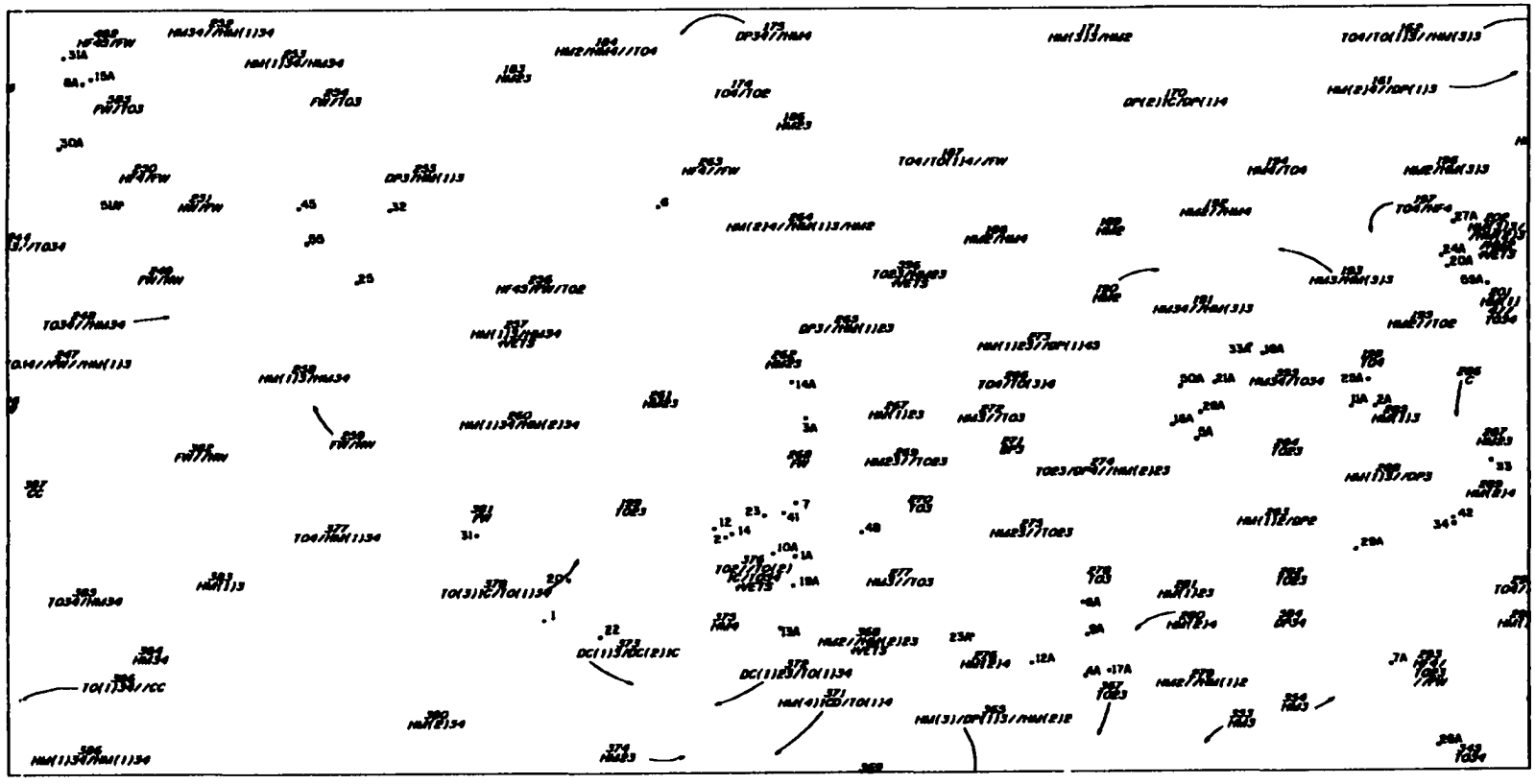
[a] More than one collar frequency per nest tree, as denoted by commas, indicates that each of the animals used the nest tree.
[b] Sapling was defined as >2 m tall and <7.5 cm dbh.
[c] Small fallen trees were defined as <7.5 cm diameter.
[d] Large fallen trees were defined as >7.5 cm diameter.
[e] Percent cover was visually estimated: class 1 = 0–10%; class 2 = 10–50%; class 3 = 50–100%.
[f] Species codes were as follows, according to MacKinnon et al. (1992):

1	hybrid white spruce	*Picea glauca x engelmannii*	15	showy aster	*Aster conspicuus*
2	lodgepole pine	*Pinus contorta*	16	twinflower	*Linnaea borealis*
3	subalpine fir	*Abies lasiocarpa*	17	fireweed	*Epilobium angustifolium*
4	trembling aspen	*Populus tremuloides*	18	red-osier dogwood	*Cornus stolonifera*
5	alder species	*Alnus* spp.	19	black twinberry	*Lonicera involucrata*
6	shrubs		20	highbush cranberry	*Viburnum edule*
7	black huckleberry	*Vaccinium membranaceum*	21	palmate coltsfoot	*Petasites palmatus*
8	mosses	e.g., *Pleurozium schreberi*	22	foam flower	*Tiarella trifoliata*
9	bunchberry	*Cornus canadensis*	23	spirea	*Spiraea* spp.
10	five-leaved bramble	*Rubus pedatus*	24	soopolallie	*Shepherdia canadensis*
11	prickly rose	*Rosa acicularis*	25	kinnikinnick	*Arctostaphylos uva-ursi*
12	purple peavine	*Lathyrus nevadensis*	26	dwarf blueberry	*Vaccinium caespitosum*
13	oak fern	*Gymnocarpium dryopteris*	27	bastard toad-flax	*Geocaulon lividum*
14	thimbleberry	*Rubus parviflorus*	28	reindeer lichen	*Cladina* spp.

Appendix C (cont'd.)

29	prince's pine	*Chimaphila umbellata*
30	Labrador tea	*Ledum groenlandicum*
31	crowberry	*Empetrum nigrum*
32	horsetails	*Equisetum* spp.
33	grasses	
34	lady fern	*Athyrium filix-femina*
35	clasping twisted stalk	*Streptopus amplexifolius*
36	ground-cedar	*Lycopodium complanatum*
37	clubmoss	*Lycopodium* spp.
38	black gooseberry	*Ribes lacustre*
39	oval-leaved blueberry	*Vaccinium ovalifolium*
40	heart-leaved arnica	*Arnica cordifolia*
41	queen's cup	*Clintonia uniflora*
42	false azalea	*Menziesia ferruginea*
43	devil's club	*Oplopanax horridus*
44	wintergreen	*Pyrola* spp.
45	paper birch	*Betula papyrifera*
46	willow	*Salix* spp.
47	trailing raspberry	*Rubus pubescens*
48	wild sasparilla	*Aralia nudicaulis*
49	false Solomon's seal	*Smilacina racemosa*

Appendix D. Ecosystem map of the study site in the Smithers Community Forest with nest tree numbers and polygon labels, and description of ecosystem types and seral stages of polygons (MacKenzie and Banner, 1991). Ecosystem maps were provided by the Prince Rupert Forest Region. Map scale is 1:15,200.



Appendix D (cont'd.)

Squirrel collar frequency	Nest tree #	Polygon #	Polygon label	Ecosystem type	Seral stage	Size of polygon (ha)
149.258	33	289	HM4	mesic	young/mature	5.50
149.258	34	289	HM4	mesic	young/mature	5.50
149.258	42	289	HM4	mesic	young/mature	5.50
149.379	55	255	DP3	dry	young/mature	25.33
149.379,149.599	25	257	HM3 + vets	mesic	young/mature with veteran trees	14.24
149.379,149.599	32	255	DP3	dry	young/mature	25.33
149.379,149.599	45	255	DP3	dry	young/mature	25.33
149.599	6	263	HF4	wet	young/mature	0.93
149.581	1	377	TO4	mesic–wet	young/mature	41.71
149.581	20	377	TO4	mesic–wet	young/mature	41.71
149.581	22	378	TO1/TO34	mesic–wet	shrubs/young/mature	2.17
149.581	31	381	FW	very wet	forested wetland	0.82
149.619	2	376	TO2 + vets	mesic–wet	pole/sapling	7.80
149.619	7	277	HM3	mesic	young/mature	5.58
149.619	12	376	TO2 + vets	mesic–wet	pole/sapling	7.80
149.619	23	376	TO2 + vets	mesic–wet	pole/sapling	7.80
149.619	41	376	TO2 + vets	mesic–wet	pole/sapling	7.80
149.619	48	277	HM3	mesic	young/mature	5.58
149.619, 150.124	14	376	TO2 + vets	mesic–wet	pole/sapling	7.80
150.124	3A	268	FW	very wet	forested wetland	2.24
150.124	14A	266	TO4	mesic–wet	young/mature	6.34
150.025	7A	293	HF4	wet	young/mature	5.88
150.025	26A	345	TO34	mesic–wet	young/mature	3.61
150.025	29A	283	HM2	mesic	pole/sapling	12.75
150.086	5A	274	TO23	mesic–wet	pole/sapling	6.57
150.086	16A	274	TO23	mesic–wet	pole/sapling	6.57
150.086	21A	274	TO23	mesic–wet	pole/sapling	6.57
150.086	28A	274	TO23	mesic–wet	pole/sapling	6.57
150.086	50A	595	HM34	mesic	young/mature	6.57

Appendix D (cont'd.)

Squirrel collar frequency	Nest tree #	Polygon #	Polygon label	Ecosystem type	Seral stage	Size of polygon (ha)
150.086	50A	595	HM34	mesic	young/mature	6.57
150.086,150.142	18A	595	HM34	mesic	young/mature	6.57
150.142	2A	285	HM3	mesic	young/mature	1.10
150.142	11A	284	TO23	mesic–wet	pole/sapling	6.46
150.142	20A	201	HM4	mesic	young/mature	3.50
150.142	24A	201	HM4	mesic	young/mature	3.50
150.142	25A	595	HM34	mesic	young/mature	6.57
150.142	27A	202	HM3 + vets	mesic	young/mature with veteran trees	10.82
150.142	55A	201	HM4	mesic	young/mature	3.50
150.166	4A	279	HM2	mesic	pole/sapling	6.38
150.166	6A	275	HM23	mesic	pole/sapling	9.09
150.166	9A	279	HM2	mesic	pole/sapling	6.38
150.166	12A	276	HM4	mesic	young/mature	4.37
150.166	17A	279	HM2	mesic	pole/sapling	6.38
150.166	23A	276	HM4	mesic	young/mature	4.37
150.450	1A	376	TO2 + vets	mesic–wet	pole/sapling with veteran trees	7.80
150.450	10A	376	TO2 + vets	mesic–wet	pole/sapling with veteran trees	7.80
150.450	13A	368	HM2 + vets	mesic	pole/sapling with veteran trees	14.63
150.450	19A	376	TO2 + vets	mesic–wet	pole/sapling with veteran trees	7.80
150.519	8A	482	HF45	wet	old growth	3.29
150.519	15A	585	FW	very wet	forested wetland	1.83
150.519	30A	482	HF45	wet	old growth	3.29
150.519	31A	482	HF45	wet	old growth	3.29
150.519	51A	249	FW	very wet	forested wetland	5.22